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TROPHIC ECOLOGY OF FISH REARING PONDS

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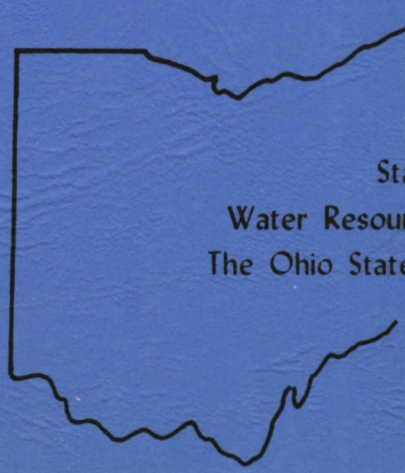

State of Ohio
Water Resources Center
The Ohio State University

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by

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Table of Contents

ABSTRACT

A three year study of the trophic dynamics of fish rearing ponds was conducted at the Hebron National Fish Hatchery, Hebron, Ohio to investigate questions concerning the interaction of various trophic levels in the plankton and to better understand the factors most responsible in determining fish yield.

Investigation of the effects of zooplankton grazing on the size structure of the phytoplankton indicated that above certain threshold levels of zooplankton biomass, zooplankton grazing can radically change the size structure of the phytoplankton community. Small flagellates were susceptible to both Daphnia and Bosmina grazing whereas small cryptomonads were only removed by Daphnia. The dynamics of resistant algal forms to grazing was not possible to predict at the species level.

The presence of filament concentrations in excess of 20% of total phytoplankton volume inhibited the egg production of Daphnia more than that of Bosmina. However, total seasonal reproductive output of both species was due to factors other than filament concentration and the effects of filaments on succession in the zooplankton is questioned.

Fish predation was found to affect the per capita egg production of Daphnia and to have a large influence on the species composition of the zooplankton community. High levels of fish predation resulted in Bosmina becoming the dominant grazer but at the same time increase the reproductive rate in Daphnia regardless of species.

Analysis of the trophic system in the fish ponds indicated that the zooplankton forage base is consistently under utilized by the fish. The low and variable yields of Northern Pike, Sauger, and Walleye were attributed to mortality of eggs and fry as a result of handling rather than due to resource limitation. We concluded that the production of these species could be increased by a factor of two simply by increasing the number of fry stocked in the ponds. Other recommendations to reduce variability in fish yields were also made. Finally, we suggest directions for further research to refine and improve present management techniques.

Key words: plankton, zooplankton, phytoplankton, algae, Bosmina, Daphnia, larval fish, grazing, productivity, bacteria, nutrients, population dynamics

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CHAPTER I

Introduction

Since the pioneering work of Lindeman (1941) the study of aquatic ecosystems has often been approached from the standpoint of energy flow between trophic compartments. Many studies have considered the quantitative interdependence between two trophic compartments. For example, the relationship between nutrient supply and algal production has been summarized by Vollenweider (1969). The interactions between phytoplankton and zooplankton (Wright 1958, Anderson et al. 1955, Gliwicz and Hillbricht-Illkowska 1972, Porter 1973), between phytoplankton and bacteria (Currie and Kalff 1984), zooplankton and bacteria (Peterson et al. 1978), and fish and zooplankton (Brooks and Dodson 1965, Gardner 1981) are well documented. However, few workers have tried an approach including three or more trophic compartments. The IBP Symposium on Productivity in Inland Waters represents a major effort in this direction. Hall, Cooper, and Werner (1970) in a classic work studied the effects of predation and resource limitation on the structure of aquatic communities. Goldman et al. (1968) studied the relationships among phytoplankton, bacteria, and zooplankton, and Wetzel et al. (1972) presented a comprehensive survey of Lake Lawrence along similar lines. Coveney et al. (1977) investigated the relationships among phytoplankton, zooplankton, bacteria, and physical/chemical factors in a small eutrophic lake in Sweden. It is becoming evident that investigations of species compositions, structure, and dynamics of any given trophic compartment must be undertaken within the context of the entire trophic system.

Within the context of the trophic structure of the aquatic system, investigations of the importance of competition and predation in determining the species succession or coexistence, community stability, and species evolution has received a great deal of attention in recent years. Data from field experiments are providing an increased understanding of the relationships between various trophic compartments and are valuable to both the ecosystem modeler and the resource manager. This report outlines results of a

field study of the trophic relationships among bacteria, phytoplankton, zooplankton, and larval fish in the planktonic community. Field studies designed to investigate this system were conducted in one acre ponds at the Hebron National Fish Hatchery, Hebron, Ohio in 1980, 1981, and 1982. The 1980 field season involved testing the effects of variable levels of fish predation on the trophic system by using fish exclosures. In 1981 and 1982 experimental manipulations consisted of varying the trophic state of selected ponds through additions of inorganic fertilizers (phosphorus, nitrogen) and/or varying the numbers of larval fish. The sampling regime was designed to provide data for detailed analyses of the interactions among various trophic compartments. In this report we discuss the results of selected experiments of this field study.

The report is divided into nine chapters. Following this introductory chapter, Chapter II presents an overview of experimental designs for each year and a summary of data collection and analysis techniques. Chapter III describes the pond systems. In Chapter IV we present the results on the effects of zooplankton grazing on the size structure and species composition of the phytoplankton. Chapter V provides data in support of Gliwicz's (1977) hypothesis concerning the effects of algal filament abundance on the reproduction of cladocerans and discusses their importance in zooplankton succession. Chapter V presents results on the effects of fish predation on the size structure and reproductive output of zooplankton. In Chapter VI a model based on field data is derived to describe the interaction between competition and predation in determining species coexistence in the zooplankton. In Chapter VII we discuss fish mortality as a function of environmental variables and make recommendations for increasing fish yield. In the final chapter (IX) directions for future research efforts are discussed.

CHAPTER II

MATERIALS AND METHODS

The study site

The study was conducted in fish rearing ponds at the Hebron National Fish Hatchery. Six ponds were used in 1980 (E180, E280, E380, E480, D280, D380), seven in 1981 (E181, E281, E481, C181, D181, D281, D381), and seven in 1982 (E182, E282, E382, E482, D182, D282, D382). With the exception of pond C1 which was substituted for E3 in 1981 the same ponds were used in each year of the study. The ponds were all very similar to one another in physical characheristics. A typical pond had a surface area of 3900 m^2 (130 x 30 m) and a volume of 4011 m^3. Maximum depth was 2.5 m and minimum depth was 1.4 m. Water levels fluctuated about $\pm$ 10 cm over the season.

The 1980 field season was used to test the effects of variations in fish predation on the planktonic community. Fish exclosures (12,000 L) were placed in each of the ponds and both the open water and exclosures were sampled. Experiments in 1981 and 1982 consisted of varying both the levels of inorganic fertilizers and fish in the ponds. The experimental manipulations for each year are summarized in Table 1. The following is a general description of the methods for sample collection and processing employed during all three field seasons.

METHODS

Phytoplankton, zooplankton, bacteria, and fish samples were taken every three days throughout the season from both the open water and enclosures. Light, temperature, and oxygen concentrations were taken with depth on the same dates. Primary productivity, alkalinity, and total phosphorus concentrations were measured every six days.

Phytoplankton samples were taken by lowering a plastic tube (1.3 x 2 cm) over the side of a boat to the sediments. This represented an integrated algal sample of the water column. Algal samples (300 ml) were preserved in the field with 5 ml acid Lugol's

Table 1. Summary of treatments for all three field seasons. Inorganic fertilizer treatments are kg/wk of additions of nitrogen: phosphorus: potassium (10:1:1). Organic fertilizers are h = hay, a = alfalfa meal, ay = active yeast. Fish species are nop = Northern Pike, sae = Sauger, wae = Walleye. No. Fish/pond indicates the number initially added to the pond. The number harvested was always significantly lower.

Treatments 1980 - 1982

POND	EXCLOSURE	INORGANIC	ORGANIC	FISH SPP	NO. FISH/POND
		1980			
E1	yes	none	h,a	sae	25,000
E2	yes	none	h,a	sae	50,000
E2	yes	none	h,a	nop	100,000
E3	yes	none	h,a	nop	200,000
E4	yes	none	h,a	sae	400,000
D2	yes	none	h,a	sae	200,000
D3	yes	none	h,a	sae	300,000
			1981		
D1	no	none	none	none	----
D2	no	7.7	h,a	nop	400,000
D3	no	none	h,a	nop	400,000
E1	no	7.7	h,a	wae	200,000
E2	no	none	h,a	wae	200,000
E4	no	none	h,a,ay	sae	200,000
C1	no	none	h,a	sae	200,000
			1982		
D3	no	none	none	none	----
D1	no	15.0	none	nop	400,000
D2	no	none	none	nop	400,000
E1	no	15.0	none	wae	250,000
E2	no	none	none	wae	250,000
E3	no	none	none	sae	400,000
E4	no	5.0	none	sae	400,000

solution, concentrated in the laboratory to 37 ml and stored in vials for subsequent counting. Cells and filaments were counted in sedimentation chambers with an inverted microscope according to Utermohl (1958). Both cells and filaments were measured with an ocular micrometer. Phytoplankton specific weight was taken as 1.0 and wet weight estimated by calculating algal volumes using length measurements and appropriate geometric formulae. Percentage of algal carbon by weight was taken from the literature (Vollenweider 1969) or estimated from the equations of Strathman (1967).

Primary productivity was measured in terms of rate of carbon fixation using C-14 sodium bicarbonate ($NaH^{14}CO_3$) as a tracer (Steeman-Nielsen 1952). Dissolved oxygen bottles were inoculated with 5 uCi $NaH^{14}CO_3$ (0.0167 uCi/ml) and incubated in situ for four hours (1000-1400). Replicate light bottles were paired with one dark bottle for each incubation both in the enclosure and in the open water. On two dates vertical series of incubations were performed in the open water of pond E2. All other incubations were performed near the surface. Samples were also incubated with 0.2 uCi C-14 for autoradiographic analysis.

To determine the uptake of tracer into the particulate fraction, 5 ml of labeled sample were taken from each DO bottle and placed in a scintillation vial. Samples were adjusted to pH=4 with 0.1 N HCL and air bubbled through the sample to remove any residual inorganic carbon (Schindler 1973). After addition of 10 ml of Aquasol-2 (fluor), radioactivity was determined by scintillation counting. Counter efficiency was determined by the channel-ratio method. Excretion of organic matter by the algae was determined by filtering 10 ml of sample through a 0.45 m Millipore filter. After acidification and bubbling, radioactivity of the filtrate was determined by liquid scintillation counting.

Depth profiles of phytoplankton productivity were calculated using light extinction data and total CO_2 determined from alkalinity and pH measurements (APHA). Daily productivity values wre obtained by multiplying productivity values from

a four-hour incubation by the factor: (total daily irradiance/irradiance during incubation). Total daily irradiance and irradiance during incubations were obtained by integrating daily light curves taken with a pyrheliometer.

To convert mean daily productivity per square meter to net uptake of carbon per 24-hour day it was assumed that: 1) C-14 methodology measures net productivity (Lewis 1974, Strickland 1960) and 2) phytoplankton respiration is equal to 10% of gross productivity at optimum light levels and is constant over the 24-hour day (Strickland 1960). Using these assumptions, respiration at optimum light intensity is equal to 10% of gross productivity or 11% of net productivity. Since the water column was well mixed during the season, this respiration value was assumed to hold over the entire water column. The total night respiration per unit volume is $P_{max}(0.11)(N)$, where P_{max} is the maximum C-14 productivity in a given incubation and (N) the total number of night hours. The net carbon gain to the phytoplankton community per square meter per 14-hour day was calculated for each sampling occasion as the mean daily productivity minus the total night respiration. The net carbon gain on other days was interpolated by using the daily light intensity for that day as a fraction of the light intensity on the nearest C-14 date and multiplying the C-14 productivity by that fraction.

Bacteria samples were taken in sterilized 20 ml vials from near the surface. Bacteria were incubated in the dark with INT dye to determine the percentage of bacteria respiring (Zimmermann et al. 1978) and then preserved with 2 ml 4% formalin solution. Bacterial abundances were estimated from direct counts using epifluorescence microscopy (Hobbie 1977). A known volume (1-5 ml) of sample was filtered onto 0.2 um Nuclepore filter and then stained with Acridine Orange (2 ml 0.01% aquesous solution) for 5 min. A section of dried filter was then placed on a microscope slide with a drop of immersion oil and covered with a cover glass. The preparation was counted on an Olympus Model Vanox fluorescent microscope at 400 or 1000X. Bacteria were enumerated in three different groups based on morphology: cocci, rods, and chains. Ten

Whipple grids were enumerated per sample. Bacteria volume was calculated using measurements of individuals of each category. Specific weight of bacteria was taken to be 1.0 to estimate fresh weight, and carbon content was assumed to be 10% of fresh weight (Sorokin and Kadota 1972). Bacterial productivity was estimated by changes in biomass over time or by corrected C-14 dark bottle uptake (Jordan and Likens 1980).

Zooplankton samples were taken by towing a metered plankton net (28 um mesh across one transect of the pond width, raising and lowering the net to integrate with depth. Samples were treated with soda water to narcotize the organisms and then preserved in a 4% formalin and sucrose solution (Haney and Hall 1973). Zooplankton were identified to species and enumerated with a dissecting microscope. Between 500 and 1500 total individuals were enumerated per sample. Rotifers were enumerated with a Sedgewick-Rafter cell on a compound microscope. Samples were enumerated until a minimum of 100 individuals of the most abundant species was counted.

Length measurements were performed on all members of the Copepoda and Cladocera. A minimum of 120 individuals was measured for each copepod species and a minimum of 30 measurements was performed on each cladoceran species. Dry weights for each instar of each species were calculated using length-weight regressions from the literature (Boucherle 1977) and zooplankton productivity calculated following Culver and DeMott (1978). The carbon/dry weight ratio was assumed to be 0.50 (Taguchi and Fukuchi 1975).

The fish community was sampled using a 3 m shore seine (1 mm mesh). The fish samples were divided into two groups. The first group was preserved immediately in the field with 4% formalin for later gut analysis. The second group was returned to the laboratory and wet weights obtained on 12-200 fish depending on their size. These fish were then oven-dried overnight at 60° C and dry weights obtained with an analytical balance. The ratio carbon/fish dry weight was assumed to be 0.50.

Analyses of gut contents were performed on 10-20 fish per date. Contents were identified to species where possible and lengths of zooplankton in the gut determined. Length of the fish gut was also measured to obtain volume estimates. Zooplankton biomass in the gut was determined as for the open water samples. The standard length of each fish was measured to the nearest 0.1 cm.

The forage ratio of the fish community on a given zooplankton species was defined as the percentage of the standing crop of that species consumed by the fish in a 24 hour period. Forage ratios were calculated as follows. The number of a given species of zooplankter from pooled fish gut analyses on a given date was converted to percentage of total zooplankton biomass in the fish gut. The fraction was then extrapolated to the amount of biomass of the species consumed by the fish over a 24-hour period from the measured increase in fish biomass over that time, assuming a gross efficiency of 40% (Carline, personal communication), and assuming the percentage of that zooplankter's biomass in the fish diet remained constant (over 24 hours). This biomass was then converted into a number of individuals of that species consumed by the fish over 24 hours. The number of individuals of a given species required to support fish growth divided by the total number of individuals of that species in the water column gives an indication of the fraction of the standing crop harvested by the fish community on a daily basis.

CHAPTER III

An Overview of Species Composition and Dynamics: 1980-1982

Species Composition

This report presents the results of selected experiments conducted during three successive field seasons (1980, 1981, 1982). The experimental season lasted from the first of April to the middle of June. Two types of ponds were used based upon season. The early ponds, used to raise Northern Pike (April 1 - May 5), were characterized by relatively low temperatures and insolation. The late ponds, used to raise Sauger and Walleye (April 15 - June 15), had relatively high temperatures and insolation. In this chapter we discuss some of the general characteristics of the system in order to highlight the similarities and differences among years.

The species present in the phytoplankton community was essentially identical in each of the years (Table 2). However, in 1980 and 1982 the phytoplankton community was dominated by the blue-green alga Aphanizomenon whereas in 1981 this alga was in low abundance. In all years of the study the small cryptomonads and small flagellate complex played a large role in the flow of energy from the phytoplankton to the zooplankton. A number of species from five different phyla show no consistent trends.

The zooplankton community was composed of six species of rotifers, four species of copepods, and eight species of cladocerans and was identical in all years of the study (Table 3). The dominant rotifers were Keratella cochlearis and K. serrulata, the dominant copepods were Cyclops bicuspidatus thomasi and C. vernalis, and the dominant cladocerans were Daphnia galeata mendotae, D. parvula, and Bosmina longirostris. The remaining species were usually present in low abundance.

Since the bacterioplankton were enumerated on the basis morphology it is not possible to make any statements concerning species composition. In terms of morphology there was little difference in the types of bacteria present in each of the three years with the

TABLE 2

PHYTOPLANKTON GENUS LIST FOR POND E2 (E1)

Chlorophyta

Dictyosphaerum
Scenedesmus
Ankistrodesmus
Selenastrum
Chlamydomonas
'Chlorococcales'
Chlorogonium
Carteria
Pediastrum
Gonium
Gloeocystis
Closterium
Tetraedron
Schroederia

Chrysophyta

Asterionella
Synedra
Dinobryon
Navicula
Diceras
Mallomonas
Poteriochromonas
Melosira
Bitridina

Cryptophyta

Cryptomonas spp.
Chroomonas

Euglenophyta

Euglena sp. (large)
Euglena sp. (small)
Trachelomonas

Cyanophyta

Aphanizomenon
Anabaena
unidentified filament

Small Flagellates

TABLE 3

ZOOPLANKTON SPECIES LIST POND E2 (E1)

Rotifera

Keratella cochlearis
K. serrulata (?)
Polyarthra
Asplanchna
Brachionus
Monostyla

Copepoda

Cyclops bicuspidatus thomasi
C. vernalis
Diaptomus oregonensis

Cladocera

Daphnia ambigua
Daphnia galeata mendotae
Daphnia parvula
Bosmina longirostris
Chydorus sphaericus

exception that in 1981 there were a number of large rods in the water column that were not present in the other two years.

Three fish species, Northern Pike (Esox lucius), Sauger (Stizostedion canadense), and Walleye (Stizostedion vitreum vitreum), were used during the study. Only the first two of these was used during 1980 and all three were used in 1981. The number of fish used varied widely (Table 1) as did the survival over the season (see Chapter 9).

Species Biomass and Dynamics.

The general trends exhibited by each of the trophic compartments is depicted in Figure 1a. Phytoplankton biomass generally declined over the season with secondary increases occurring during the beginning of June in some of the ponds (e.g. C181, E481). Maximal phytoplankton biomass occurred in the spring and varied between 10 and 20 ml/m^3.

Bacterial biomass exhibited two different types of dynamics. In the first bacteria generally mimicked the phytoplankton, with early spring maxima followed by a general decline to low values. This occurred mainly in 1980. In the other type there was a large initial bacterial biomass which declined to a minimum about the middle of May and then exhibited a large increase in the first part of June. This was observed in 1981 and to an extent in 1982.

The maximum zooplankton biomass varied between 0.8 and 5.9 mg dry weight per liter. Daphnia spp. always accounted for most of the zooplankton biomass at these peaks. These species were followed by copepods, Bosmina, and rotifers in order of importance. In general the early spring was dominated by copepods and rotifers and these gave way about the middle of May to cladocerans. This pattern was observed consistently in all years.

The larval fish were placed in the ponds as swim-up fry or as eyed eggs. The fish grew to varying degrees and were usually on the order of 5 - 7 cm at time of harvest.

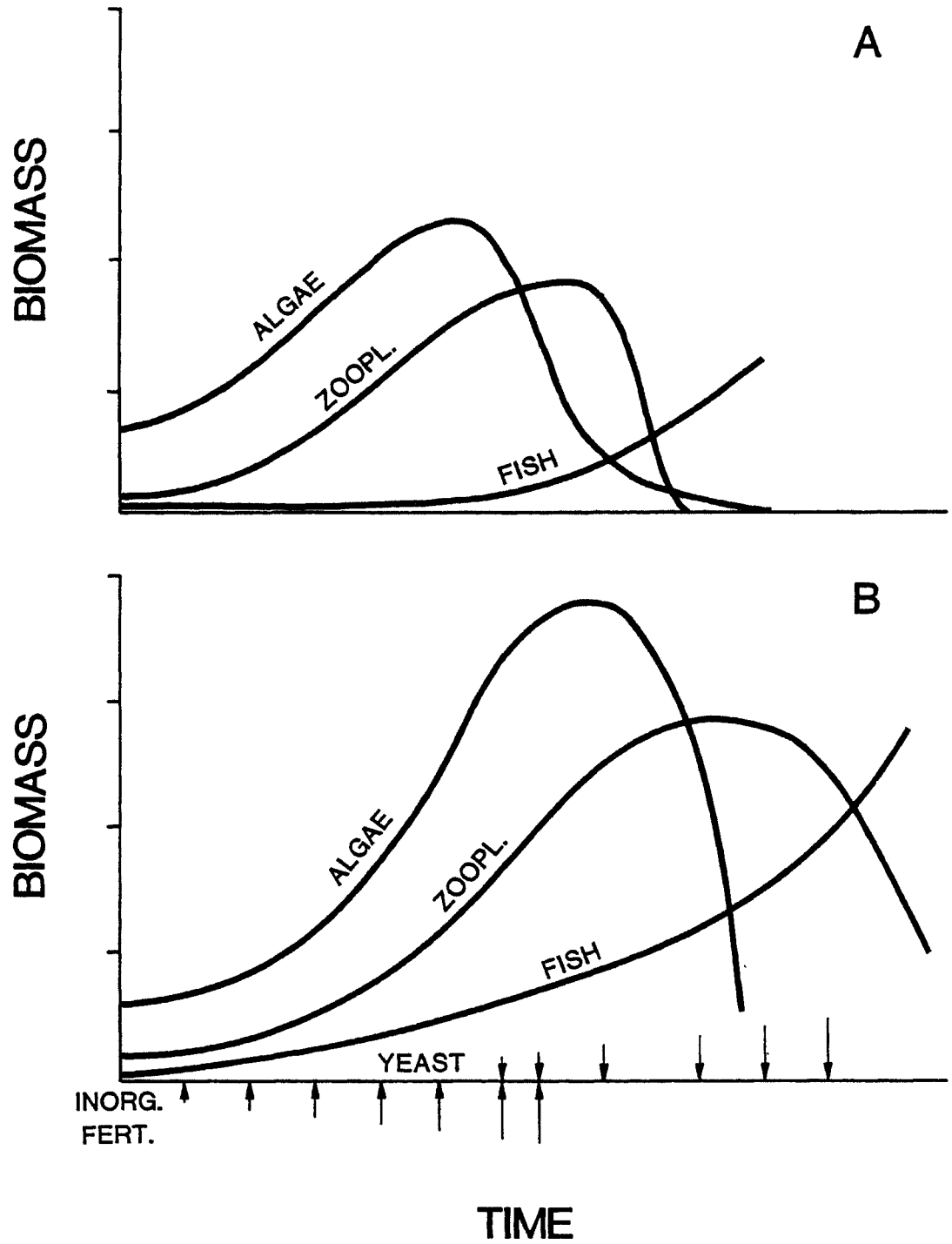

Figure 1 a. General trends exhibited by algal, zooplankton, and fish biomasses in the fish ponds over time. The maximum standing crop of zooplankton generally occurred after peak algal biomass. Fish biomass increased exponentially with time.

b. Proposed result of fertilization with inorganics (N,P,K) and active yeast.

The fish grew nearly an order of magnitude in length and two orders of magnitude in weight during the season.

Experiments designed to investigate the dynamics of the plankton were also used in attempts to improve the yield of fish biomass from the system and reduce between pond variablity in fish survived. The basic idea behind these efforts is shown in Figure 1b. The level of phytoplankton and zooplankton can be increased and prolonged with serial additions of inorganic and/or organic fertilizer. The addition of fertilizer in small doses at frequent intervals not only increases the yield of fish biomass but also reduces the varability in yield.

CHAPTER III

Evidence for Size-Selective Grazing by Zooplankton

Introduction

Numerous factors are responsible for seasonal succession in the phytoplankton. Among these are light, temperature, nutrients, parasitism, and their interactions. In addition, size-selective grazing on certain size classes of phytoplankton by zooplankton has been hypothesized to account for relative algal species abundances and succession (Porter 1977). Field experiments have shown that herbivory influences the make-up of the phytoplankton (McCauley and Briand 1979). Studies of natural populations have demonstrated that invertebrate predators can control Daphnia populations at certain times and allow small algae to flourish (Lampert and Schober 1982) or that high fish population levels may control Daphnia and allow the growth of a larger total standing crop of phytoplankton (Lynch and Shapiro 1981). In this chapter we investigate the impact of cladoceran zooplankton grazing on the size structure and species composition of the phytoplankton community.

Results

For analysis of the size structure of the phytoplankton the algal species were grouped into size classes based on cell volumes. The filamentous species were placed in one class and the non-filamentous species were divided into three classes: class 1, less that 100 m^3/cell; class 2, 100-400 m^3/cell; class 3, greater than 400 m^3/cell. The dividing lines between the latter categories were at ca. 5 and 9 um equivalent spherical diameters.

The experimental ponds were divided into three different groups according to the size and composition of the zooplankton community. Group 1 (ponds E481, C181, D181) was characterized by a large standing crop of cladocerans dominated by Daphnia spp.

Group II (ponds E181, E281) had a large standing crop of cladocerans dominated by Bosmina and Group III (ponds E382, E482) had relatively small standing crops composed mostly of Daphnia spp. In all of these ponds the total standing crop of cladocerans exhibited increases beginning about the middle of May (Fig. 2 a, b, c). Total phytoplankton volumes generally declined from initial values of 10-20 ml/m^{-3} to less than 1 ml/m^3 by the end of May (Fig. 3). The exception to this pattern was pond E481 in which the total algal volumes increased beginning near the end of May.

The increases in zooplankton biomass corresponded to changes in the size structure of the phytoplankton community. The following paragraphs summarize the observed patterns of change in the phytoplankton volume frequencies during periods of increasing zooplankton grazing for the three groups.

Group I. These ponds had large standing crops of zooplankton dominated by Daphnia spp. During the increase in Daphnia populations there was a corresponding decrease in the class 3 phytoplankton accompanied by increases in size classes 1 and 2 (Fig. 4 a, b, c). The class 3 algae were composed mainly of small cryptomonads, the class 2 were mostly Schroederia and Chroomonas, and the class 1 contained Scenedesmus, Ankistrodesmus, Oocystis, Sphaerocystis, and Dictyosphaerium.

Group II. These ponds, dominated by large standing crops of Bosmina exhibited a trend opposite to that of Group I. As the Bosmina populations increased size class 3 phytoplankton also increased and this was accompanied by a decreased in size classes 1 and 2 (Fig. 4d,e). The class 3 algae were almost exclusively small cryptomonads, the class 2 was mostly Schroederia, and class 1 contained Scenedesmus, Oocystis, Actinastrum, and Sphaerocystis.

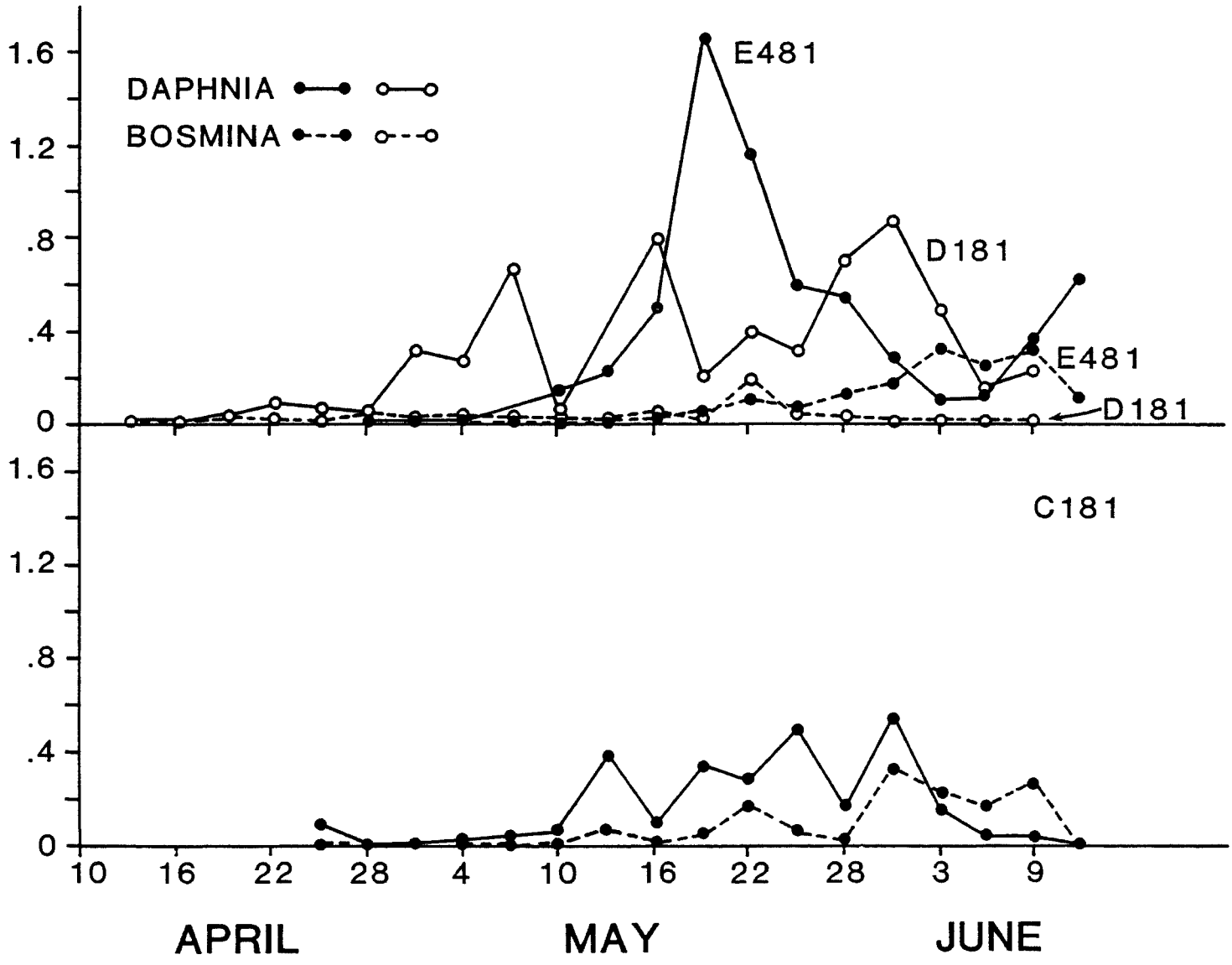

Figure 2a. Standing crop of Daphnia and Bosmina biomass in the Group I ponds (C181, D181, E481) over time. Daphnia was the dominant grazer in these ponds.

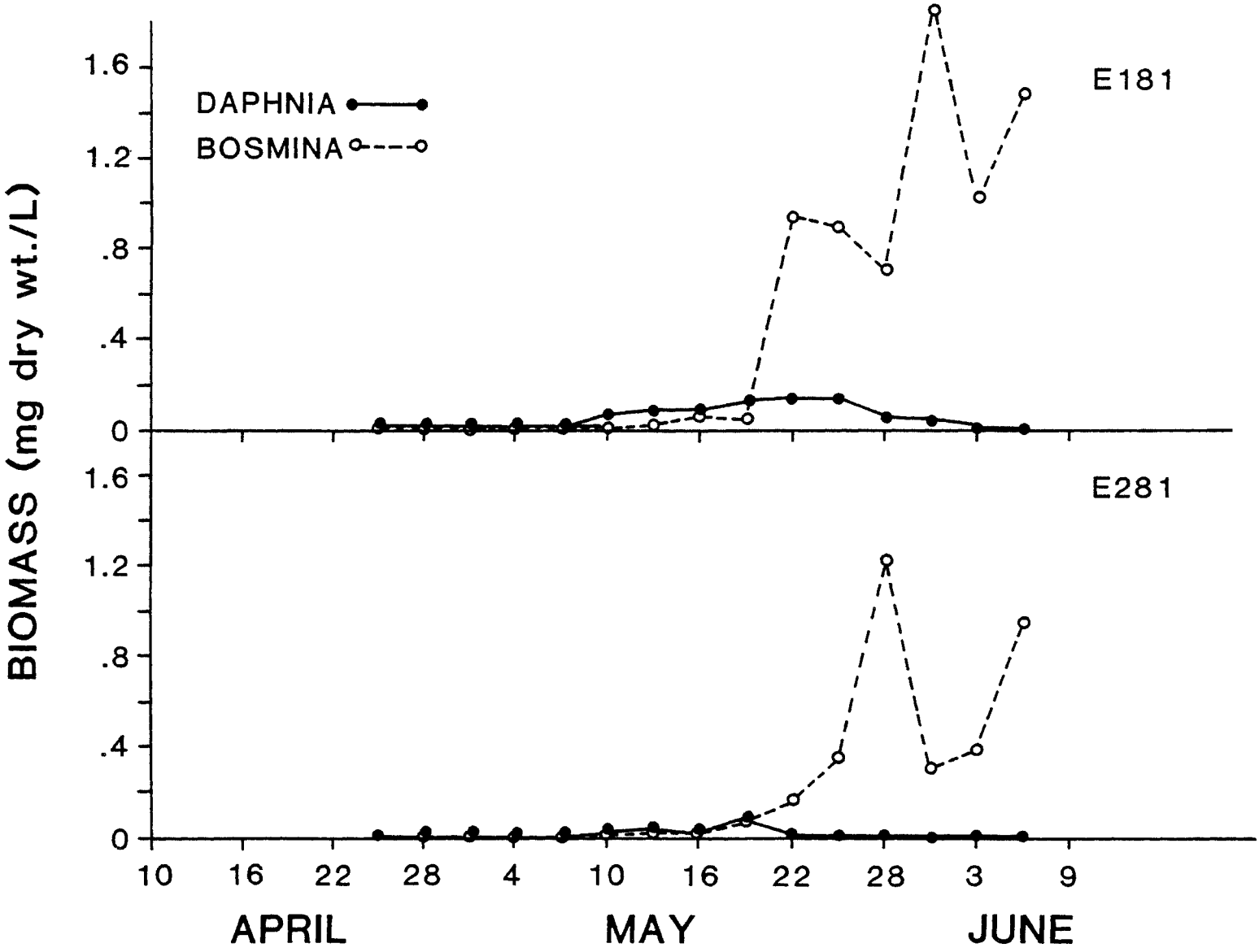

Figure 2 b. Standing crop of Daphnia and Bosmina biomass in the Group II ponds (E181, E281) over time. Bosmina was the dominant grazer in these ponds.

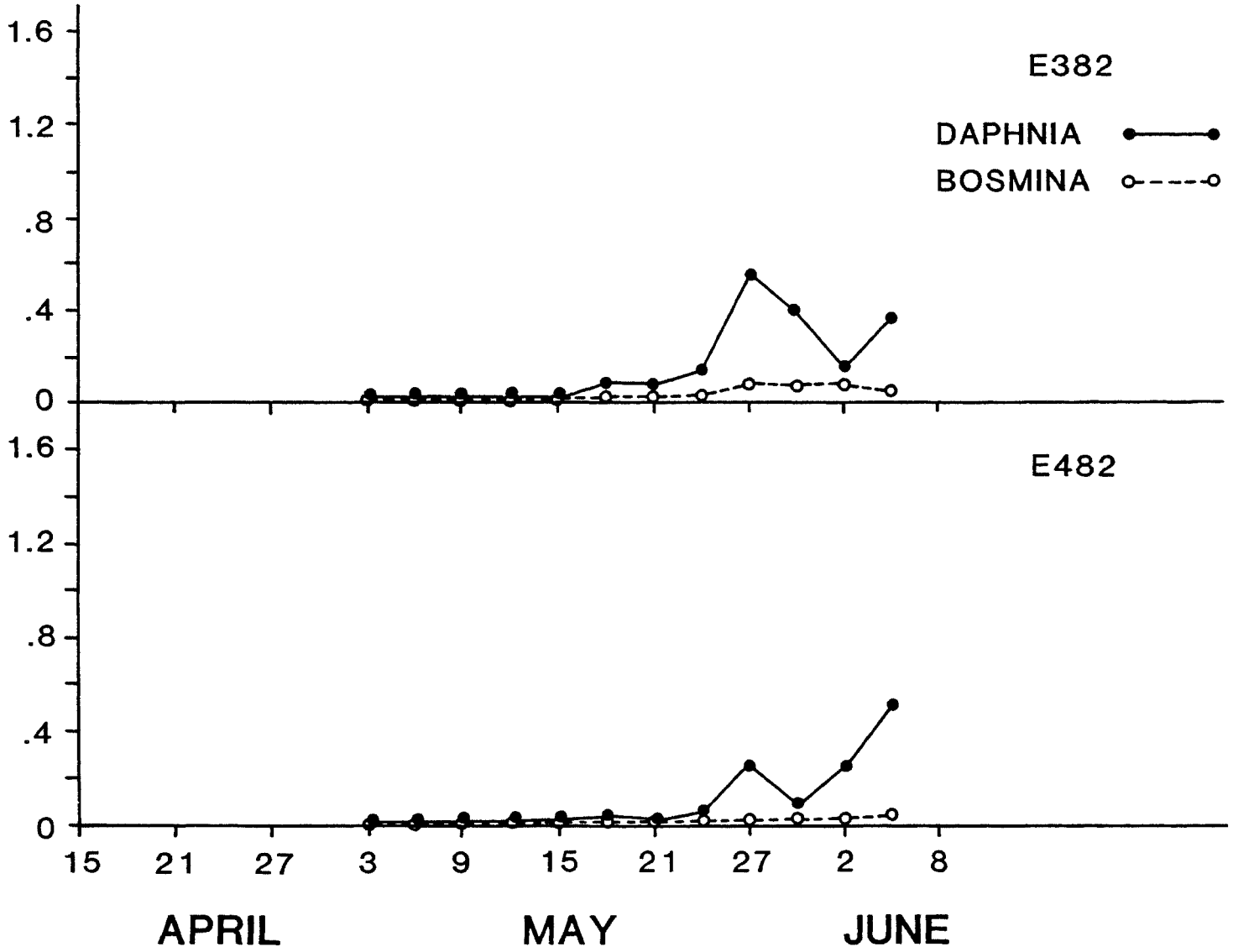

Figure 2 c. Standing crop of Daphnia and Bosmina biomass in the Group III ponds (E382, E482) over time. Both genera were in relatively low abundance in these ponds.

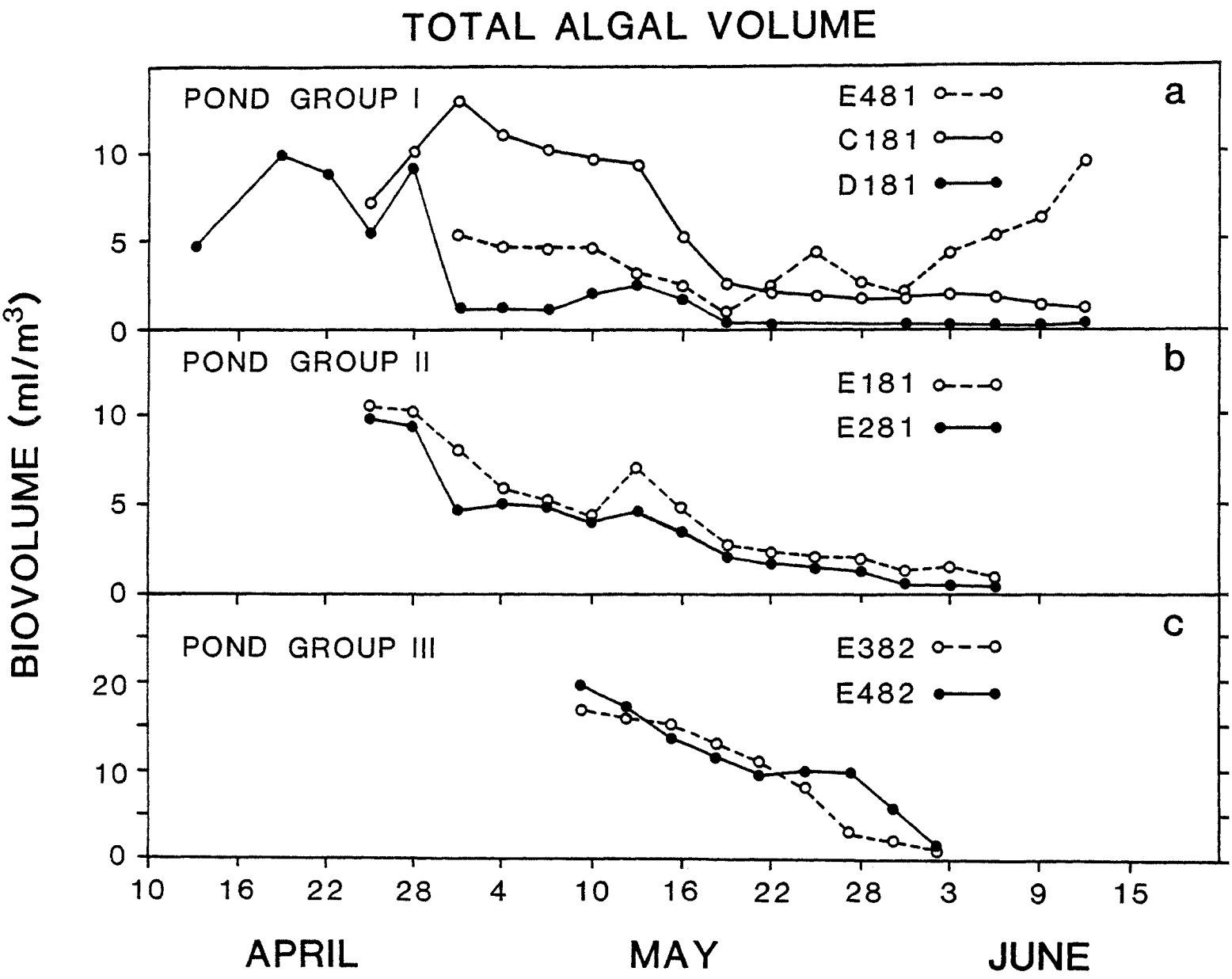

Figure 3. Total phytoplankton volume over time in each of the pond groups. Total volume generally declined over the season with the exception of pond E481.

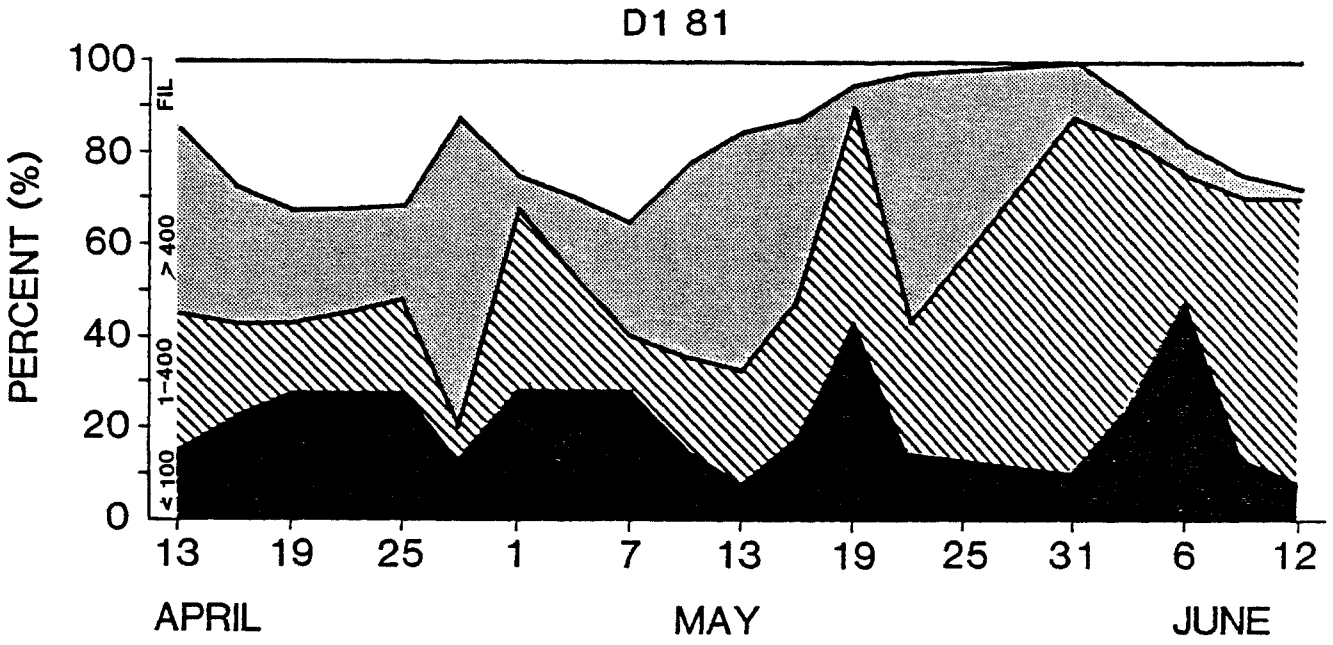

Figure 4 a. Cumulative volume frequencies of algal volume classes 1-4 in the Group 1 ponds over time. The class three algae showed a decline in relative abundance during periods of intense Daphnia grazing. Pond = D181

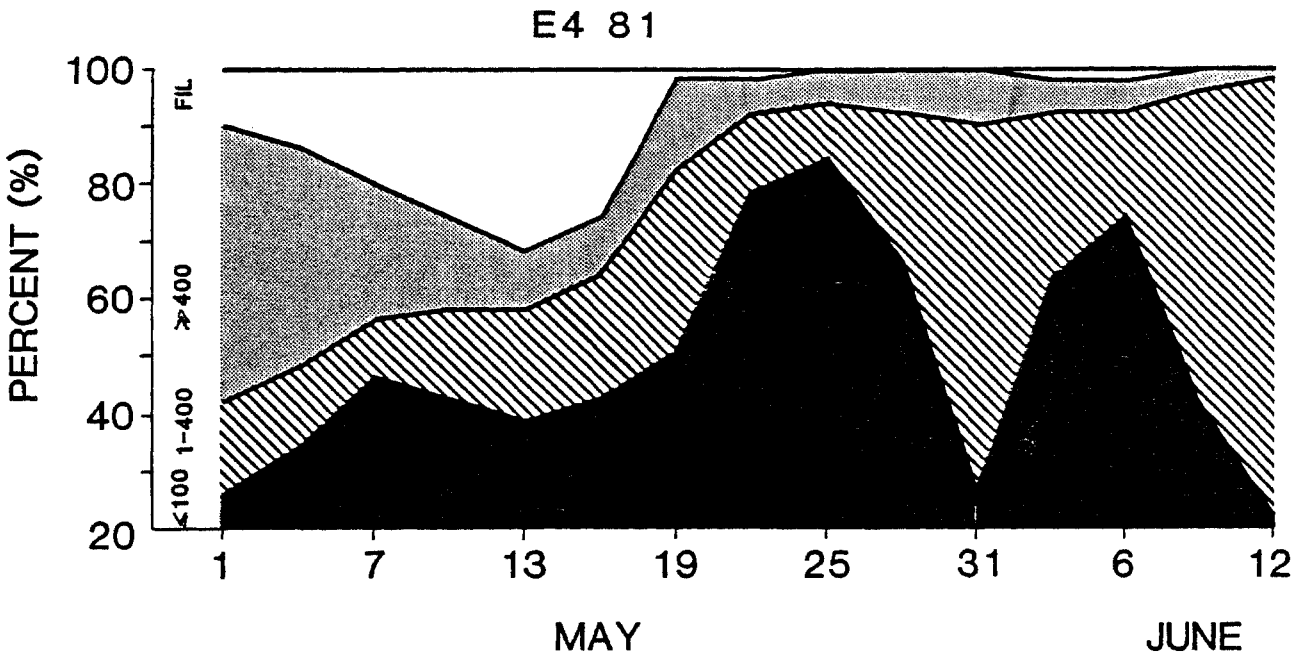

Figure 4 b. Cumulative volume frequencies of algal volume classes 1-4 in the Group 1 ponds over time. The class three algae showed a decline in relative abundance during periods of intense Daphnia grazing. Pond = E481

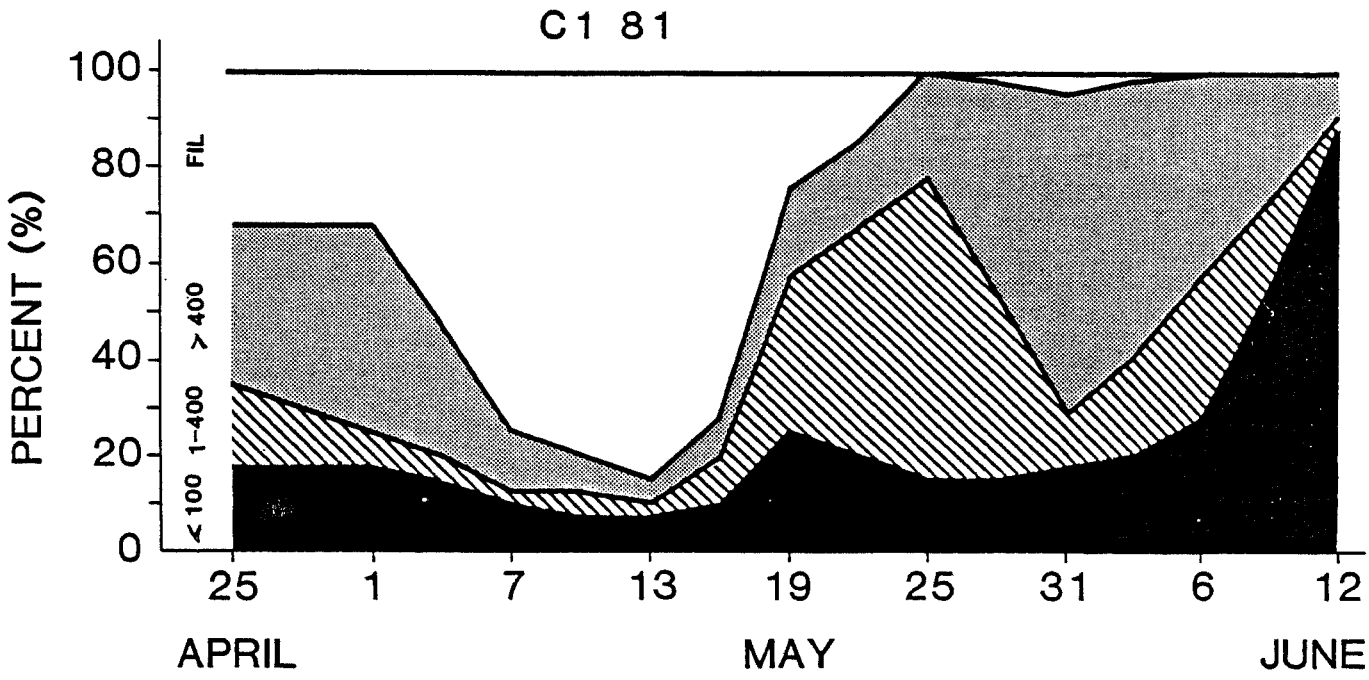

Figure 4 c. Cumulative volume frequencies of algal volume classes 1-4 in the Group I ponds over time. The class three algae showed a decline in relative abundance during periods of intense Daphnia grazing. Pond = C181

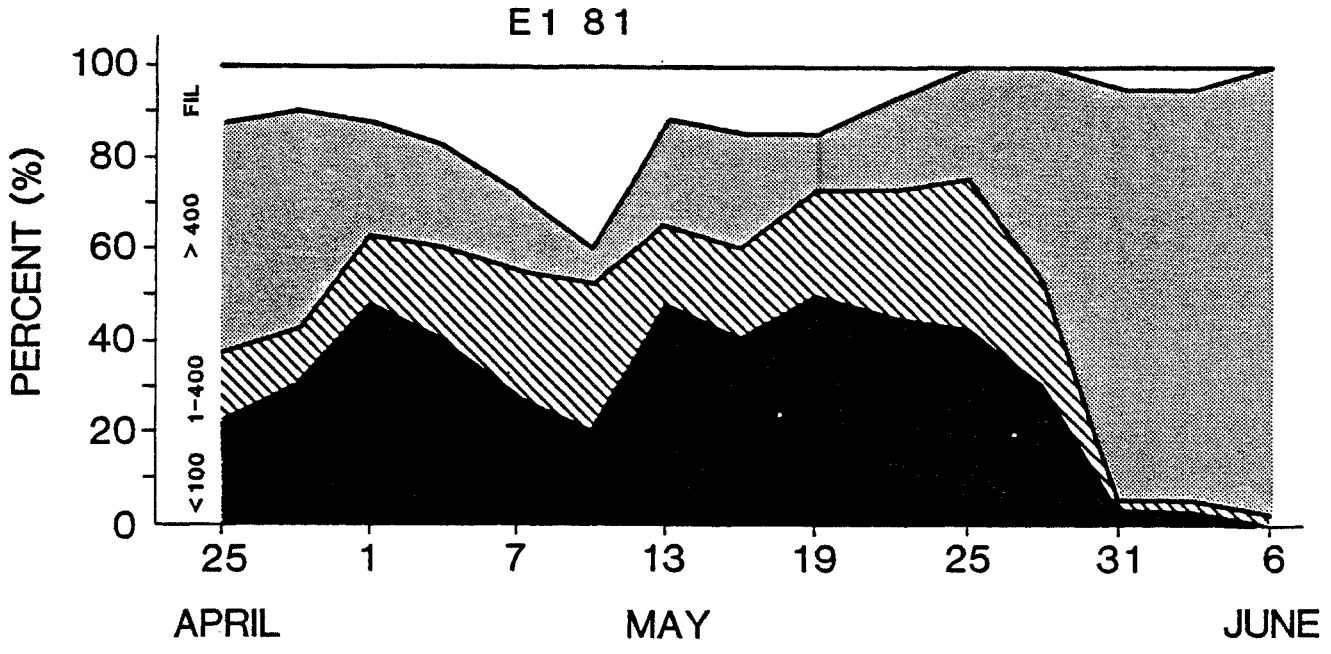

Figure 4 d. Cumulative volume frequencies of algal volume classes 1-4 in the Group II ponds over time. The class 3 algae increased in relative abunance during periods of intense Bosmina grazing. Pond = E181

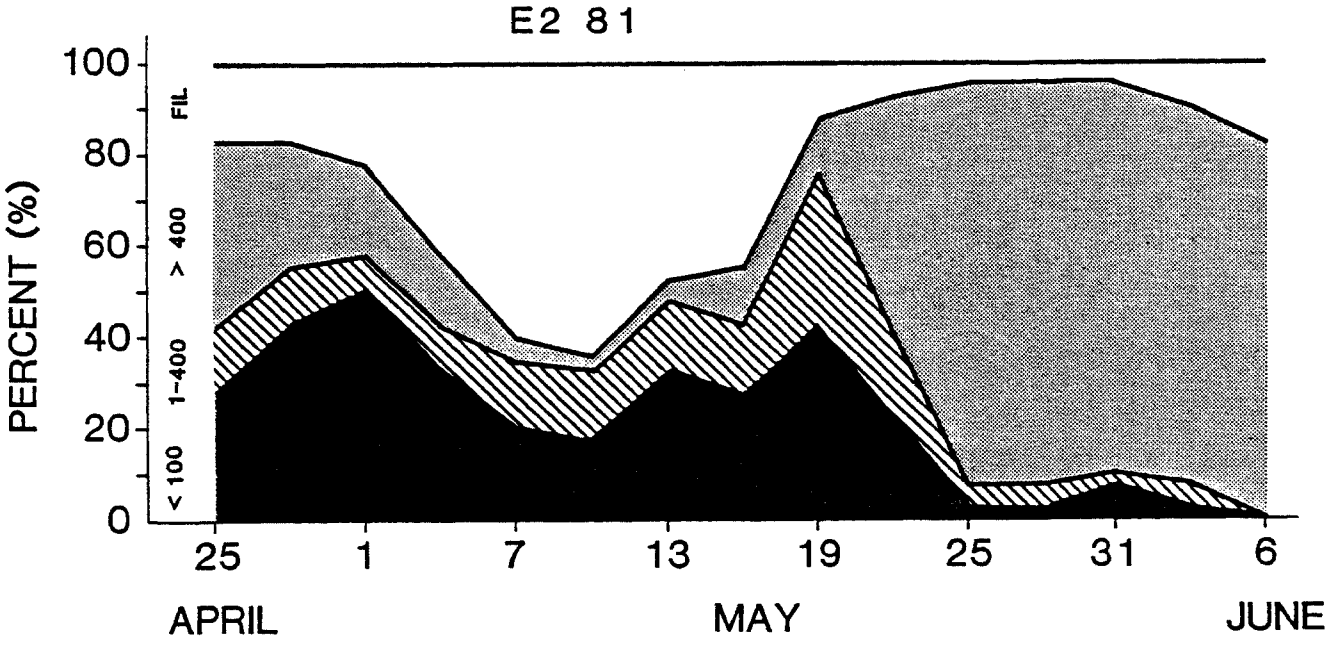

Figure 4 e. Cumulative volume frequencies of algal volume classes 1-4 in the Group II ponds over time. The class 3 algae increased in relative abundance during periods of intense Bosmina grazing. Pond = E281

Group III. These ponds had low standing stocks of zooplankton compared to the above two groups. In these ponds the size classes I and 2 became co-dominant, with size class I of lesser importance (Fig. 4f,g). The class 3 algae were mainly small and large cryptomonads, class 2 contained spiny Chlorococcales and Schroederia, and class I contained Actinastrum, Scenedesmus, small flagellates, Ankistrodesmus, Oocystis, Dictyosphaerium, and Sphaerocystis.

In all of the ponds the percentage of filamentous algae during this period generally declined to less than 10% of the total algal volume (Fig. 4.)

Discussion

For zooplankton grazing to affect the species composition of the phytoplankton community two conditions must be satisfied. First the grazing pressure of the zooplankton must be large enough to constitute the largest factor in the death rate of a phytoplankton population and secondly the grazing must be selective, i.e. certain algae must be relatively more immune to grazing than others. The species composition of the major grazers will further influence the precise effects of grazing pressure because different zooplankters presumably have different filtering capabilities.

The data presented here susgest to what extent the absolute and species-specific zooplankton grazing rates affect the size structure of the algal community. During the times of increasing zooplankton grazing pressure, Daphnia and/or Bosmina accounted for over 90% of the filtering pressure in all of the ponds. The differences in pond Groups I and II illustrate the affects of Daphnia as compared to Bosmina grazing on the phytoplankton community. The most striking difference was the selective removal of the class 3 algae by Daphnia whereas Bosmina were unable to successfully graze this size class (Fig. 4 a-f). This difference was not due to differences in the size of the standing crop of zooplankton because the biomass of Bosmina in pond E181 and E281 was equal to or greater than that of Daphnia in the Group I ponds (Fig. 2 a,b).

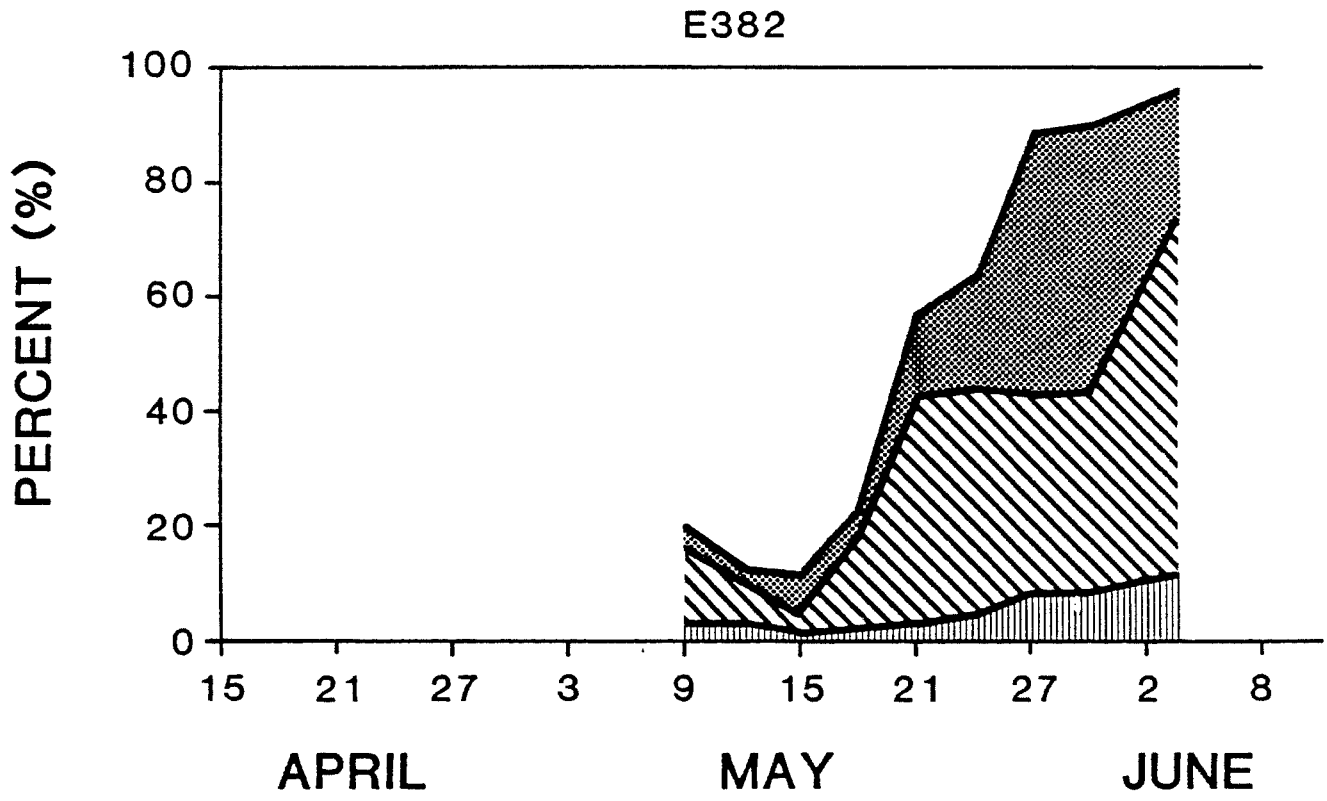

Figure 4 f. Cumulative volume frequencies of algal volume classes I-4 in the Group IV ponds. In the absence of intense grazing size classes I-3 became co-dominant. Pond = E382

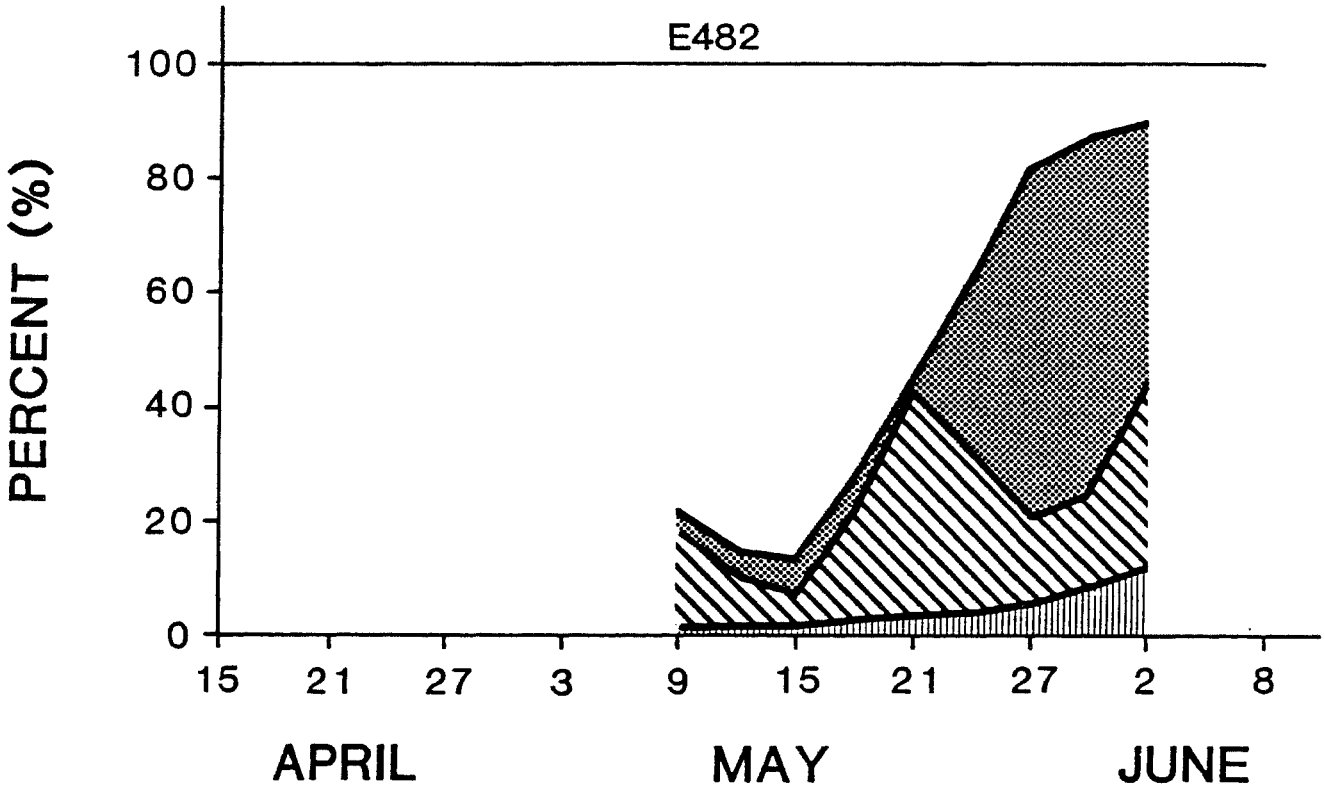

Figure 4 g. Cumulative volume frequencies of algal volume classes I-4 in the Group IV ponds. In the absence of intense grazing size Classes I-3 became co-dominant. Pond = E482

In Group III ponds zooplankton grazing had minimal affect on the phytoplankton size-frequency structure. In these ponds the proportion of each size class remained fairly constant throughout the period of most intense grazing (Fig. 4 f,g). Even though Daphnia was the major filtrator (Fig. 2 c) the standing crop was not large enough to cause significant shifts in the size frequency of the algae as evidenced by the persistence of the class 3 algae (Fig. 4 f,g).

Although the intensity of zooplankton grazing and the nature of the dominant grazer appear to cause changes in the size structure of the algal community it is not possible to predict the exact course of species succession. However, there are general trends concerning the persistence and disappearance of certain algal species that do emerge. In particular, the small cryptomonads and small flagellates are closely correlated to the intensity of zooplankton grazing. The height of the secondary peaks of the small cryptomonads in late May is negatively related to intense Daphnia grazing but not to Bosmina grazing. In the Group II and III ponds the small cryptomonads had large secondary peaks whereas in the Group I ponds they did not (Fig. 5). Thus the persistence of the small cryptomonads is dependent upon both the intensity of zooplankton grazing and the species of the dominant grazer.

The small flagellate complex is susceptible to both Daphnia and Bosmina grazing and therefore its persistence depends on the total grazing pressure independent of zooplankton species. In both Groups I and II the flagellates were effectively removed from the water column while in the Group III ponds they showed a large secondary increase (Fig. 6). The exception to this pattern seen in pond E181 (Fig. 6 b) was due to the additions of inorganic nutrients to the pond.

The selective removal of certain algal species has the direct effect of changing the size structure of the community. In addition, this should have the indirect effect of providing a net gain in resources (e.g. nutrients) to the resistant forms. These species would then be expected to show an enhanced response to selective zooplankton grazing. For the group of algae which appeared to be resistant to zooplankton grazing there was

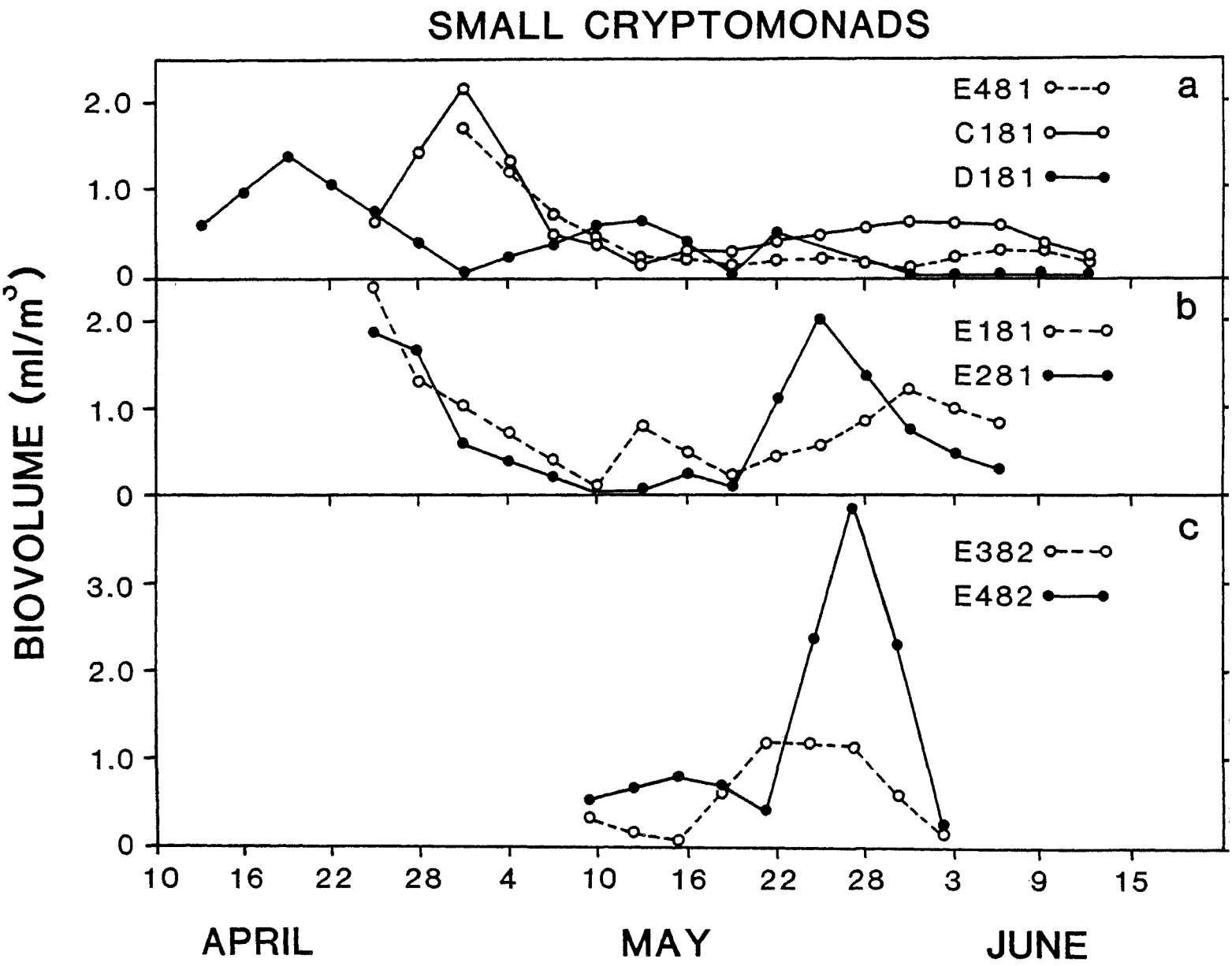

Figure 5. Biovolume of small cryptomonads over time in: a) the Group I ponds, b) the Group II ponds, and c) the Group III ponds.

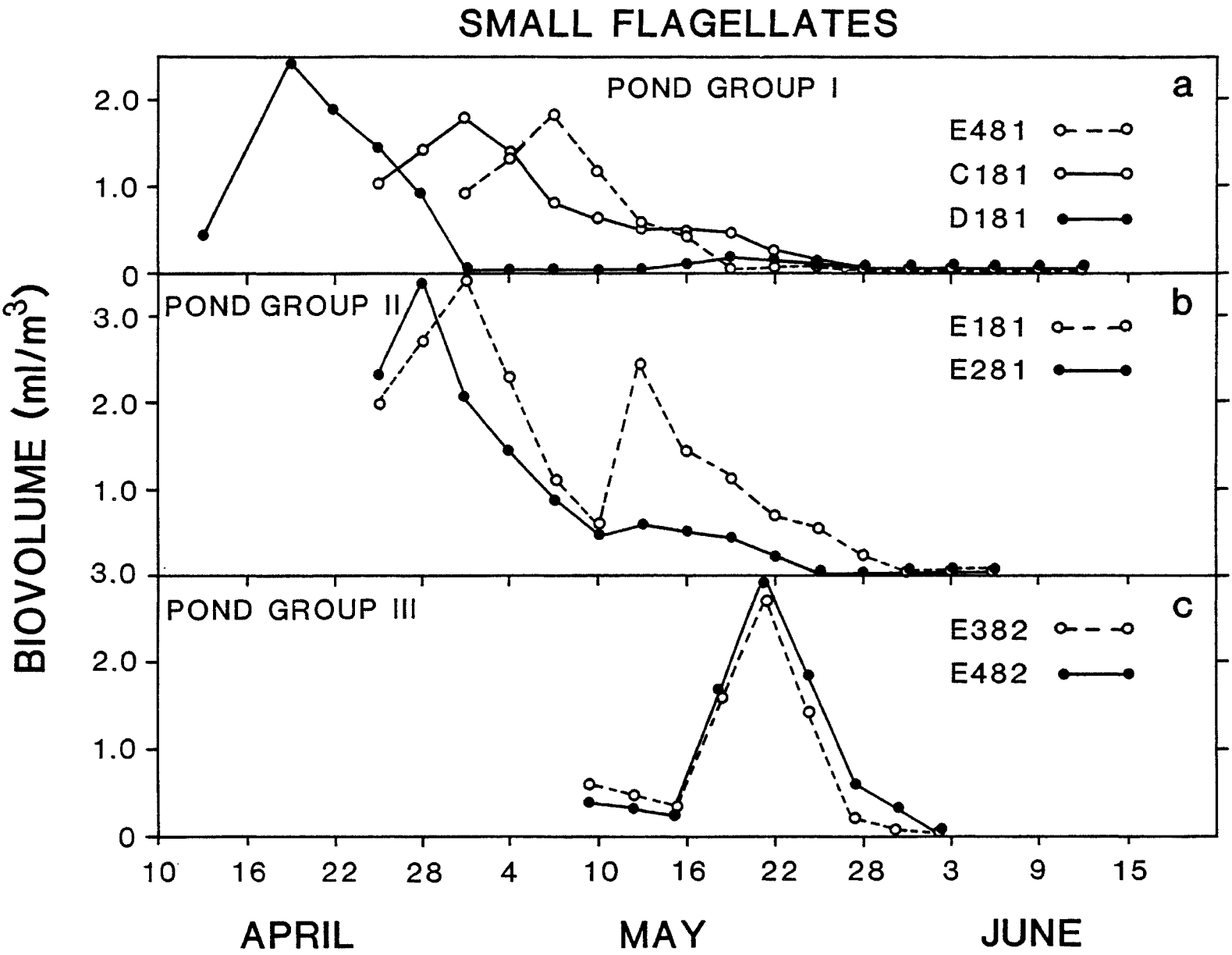

Figure 6. Biovolume of small flagellates over time in: a) the Group I ponds, b) the Group II ponds, and c) the Group III ponds.

so consistent pattern in response to zooplankton grazing. For example, the colonial Sphaerocystis, which is fairly resistant to grazing, increased dramatically in pond E481 with the increase in zooplankton grazing pressure but increased only slightly or not at all in pond D181 and C181 or any of the Group II ponds (Fig. 7). Thus a clear response of algae at the species level is difficult to predict based soley on zooplankton grazing. This is not surprising considering the importance of light, temperature, and nutrients to competitive interactions in the phytoplankton.

In summary, above a certain threshold level of zooplankton biomass the size structure of the phytoplankton community can be radically changed by grazing of zooplankton. Furthermore, the changes in the size structure are dependent not only on the intensity of the grazing pressure but also on the nature of the dominant grazer. Daphnia alone can remove class 3 algae from the water column whereas both Daphnia and Bosmina can remove class I algae. While it is possible to predict the loss of certain species of algae (e.g. small cryptomonads, small flagellates) on the basis of grazing intensity, the response of the resistent forms is much less predictable.

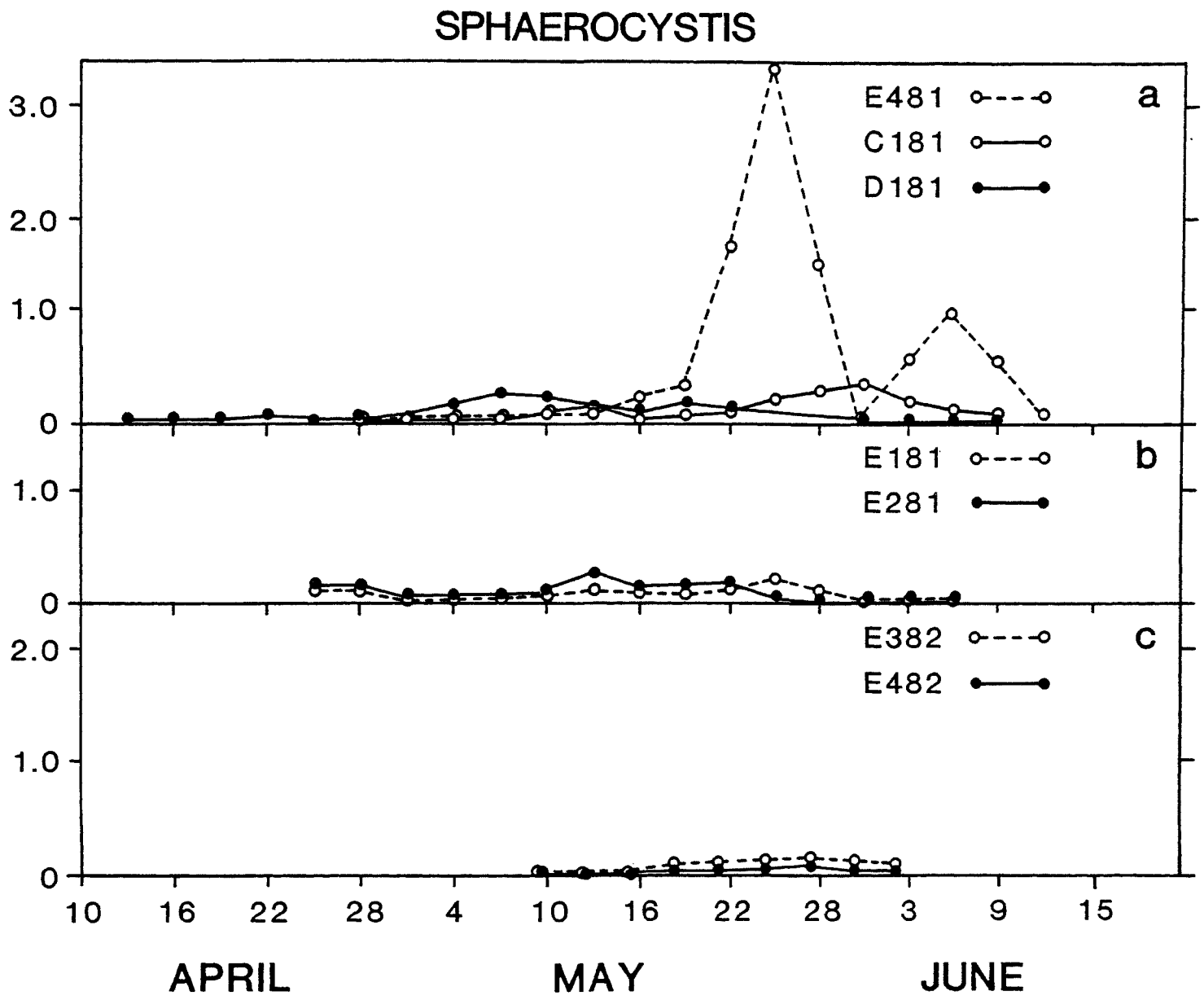

Figure 7. Biovolume of Sphaerocystis over time in: a) the Group I ponds, b) the Group II ponds, c) the Group III ponds.

CHAPTER IV

The Fecundity Ratios of *Daphnia* and *Bosmina* as a Function of Filamentous Algal Concentration

Introduction

In the previous chapter we considered the effects of zooplankton grazing on the size structure of the phytoplankton community. Gliwicz (1977) has hypothesized that the size structure of the phytoplankton, namely the abundance of filamentous forms, determines the seasonal succession in the zooplankton. To explain this effect he proposed that large zooplankters suffer a greater reduction in filtering (and hence ingestion) rate than small zooplankters with increasing concentrations of net (i.e. large and filamentous) algae. The differential effect on filtering rates is due to a simple mechanical interference with the filtering apparatus. Larger zooplankton e.g. *Daphnia* can bring net plankton into the food groove and must then eject the cells whereas net plankton will not pass into the food groove of smaller (e.g. *Bosmina*) zooplankters. Consequently, the higher ejection rate for the larger organisms results in a net decrease in ingestion rate and fecundity. Gliwicz went further and suggested that the increases in net phytoplankton generally associated with increased nutrient loading implied that as a lake become more eutrophic the composition of the zooplankton community would shift toward smaller species.

In this chapter we investigate the relative competitive abilities of a large (*Daphnia*) versus a small (*Bosmina*) zooplankter in relation to the composition and size structure of the phytoplankton community. In addition, the effects of total carbon flow into the resource base (bacteria + algae) on seasonal reproduction and succession of these species is discussed.

The Fecundity Ratio

To determine the effects of algal filament concentration on the fecundity of these species it is necessary to first derive a simple comparative measure of reproductive output. Since these organisms differ in size (Bosmina: .10 - .75 mm, Daphnia: .20 - 2.5 mm) and therefore in maximal fecundity or brood size, it is not sufficient to simply compare their absolute fecundities. The following describes is relative measure of fecundity, the difference in the fecundity ratios (DFR) used in this analysis.

The maximal possible egg production of a cladoceran population is calculated by multiplying the maximum possible number of eggs per female in a given size class by the number of individuals in that size class. The relationship defining the maximum number of eggs per female as a function of size was extracted from a plot of the eggs per female versus length for data pooled for an entire year. A line was fitted to the trend suggested by the scatter of points to obtain an equation relating the maximum brood size to the length of a female. For Daphnia galeata mendotae this equation was,

$$Y = 19.518(L) - 15.327$$

where Y is the maximum number of eggs possible for a female of length (L). Similar curves were constructed for D. parvula, D. ambigua, and Bosmina longirostris (Vaga et al. 1984).

The fecundity ratio of species, FR(i), is defined as the ratio of the observed number of eggs in a sample for that species to the theoretical maximum for that population.

$$FR(i) = \frac{ONE(i)}{N_{ij}\ Y_{ij}} \qquad \text{Equation 1}$$

where ONE(i) is the observed number of eggs in a sample for species and N is the number of females of species i of length j, Y_{ij} is the maximum possible number of eggs/female of species i and length j.

When the FR(i) is close to 1.0 the population is reproducing at close to its maximal rate and when it is 0.0 reproduction has ceased. The value of FR(i) is undefined when there are no adults in the population.

Comparison of the fecundities of two species of different body size can be achieved by defining a new variable, the difference in the fecundity ratios of the species (DFR),

$$DFR = FR(1) - FR(2) \qquad \text{Equation 2}$$

where the subscripts refer to different species. This provides a relative measure of the two species' reproductive outputs in terms of their respective maxima which is based on the size frequency distributions of the populations.

In this analysis the DFR was defined by subtracting the Bosmina FR from the Daphnia FR. Values of DFR greater that zero indicate that the Daphnia population has a greater relative reproductive rate than Bosmina and when DFR is less than zero the two populations are equally limited (or unlimited). Since DFR is a relative measure it does not indicate the absolute reproductive rates of the populations and cannot be used to investigate questions concerning species coexistence. This will be discussed further in the following sections. The samples for which FR is undefined will be noted when they occur. As the egg development times as a function of temperature for these species are similar, the effects of temperature can be ignored.

Results

The species present in the phytoplankton community in 1980 and 1981 were essentially identical (Munch in prep). Maximal total phytoplankton and bacterial volume (PBV) varied among ponds but in all cases exhibited a general decline over the season

(Fig. 8). Values of PBV were greatest in E10 and E2E followed by C1 and D1 (Fig. 8). The percentage of PBV composed of filaments (mainly Aphanizomenon) declined over the season. Filament volume in pond D1 never exceeded 20%. Total carbon fixation (light counts) by both algae and bacteria was greatest in E10 followed by E2E, C1, and D1 (Fig. 8). Average filament length in 1980 showed a consistent decrease through June 1 and coincided with the decline in Aphanizomenon abundance (Fig. 8).

As a general rule, for forage base volumes greater than 2 ml/m^3 the value of DFR was less than zero for high filament concentrations and increased with decreasing filament volume (Fig. 8). The difference in the fecundity ratios (DFR) of Daphnia and Bosmina was consistently less than zero in pond E10 until May 23 after which it oscillated about the zero line. A similar pattern was observed in pond E2E. The value of DFR in pond C1 increased to a maximum on May 1 and steadily declined to a value of - 0.19 on May 16, then increased to a value of 0.5 on June 9 (Fig. 8). In pond D1, DFR slowly declined from April 17 to May 7 and then oscillated about zero.

Daphnia biomass was low in E10 and E2E until May 26 when populations increased in a dramatic fashion (Fig. 9). In pond C1 the population increased slowly after May 10 and in pond D1 the population oscillated, with peaks occurring on May 7, 16, and 31 (Fig. 9). The biomass of Bosmina increased steadily in ponds E10 and E2E from low values to maxima on May 29 (Fig. 9). In pond C1 Bosmina showed peaks on May 22, 31, and June 6 while in pond D1 Bosmina increased until May 22 and then rapidly declined (Fig. 8).

There was a marked difference in the absolute magnitude of the biomass and egg production of these species between 1980 and 1981. In 1980 maximum Daphnia biomass peaked at over 5 mg dry weight/L and egg production peared at over 125 eggs/L. In contrast the maximum Daphnia biomass in 1981 was just over 0.85 mg dry weight/L (pond D1) and maximum egg abundance was about 30 eggs/L. The maximum standing crop of Bosmina in 1980 was about 0.6 mg dry weight/L (pond E2E) and egg abundances peaked at almost 70 eggs/L (Fig. 9). In 1981 Bosmina biomass was 0.35 mg dry weight/L and egg abundances only reached 30/L (pond C1) (Fig. 9).

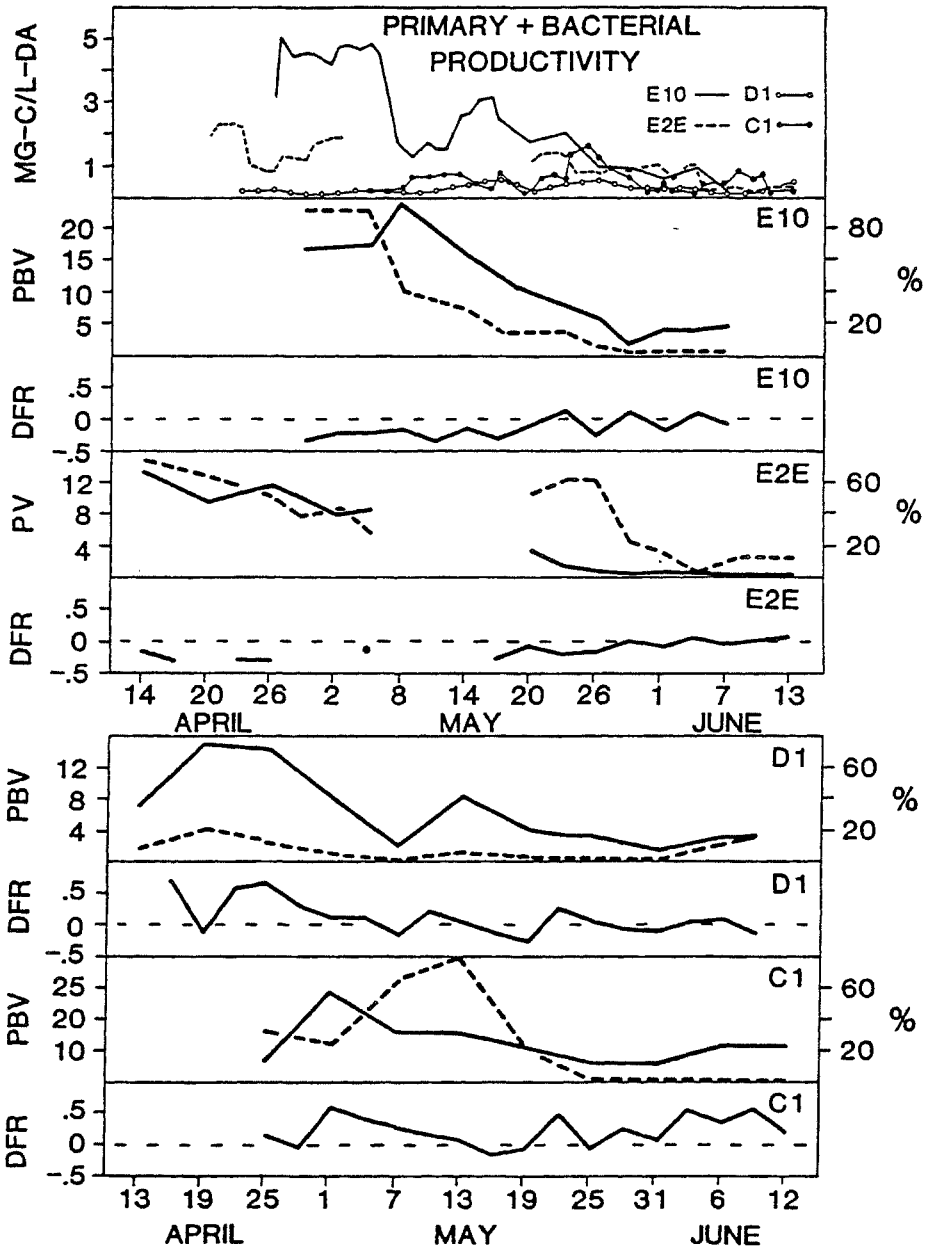

Figure 8. Top panel: Total algal and bacterial productivity for ponds, E10, E2E, C1, and D1. Lower Panels: Total phytoplankton and bacterial volume PBV (———), percentage of PBV as filaments (- - - -), and difference in the fecundity ratios (DFR) of Bosmina and Daphnia over time for these same ponds. See text for explanation. (PV in pond E2E refers of total algal volume only.)

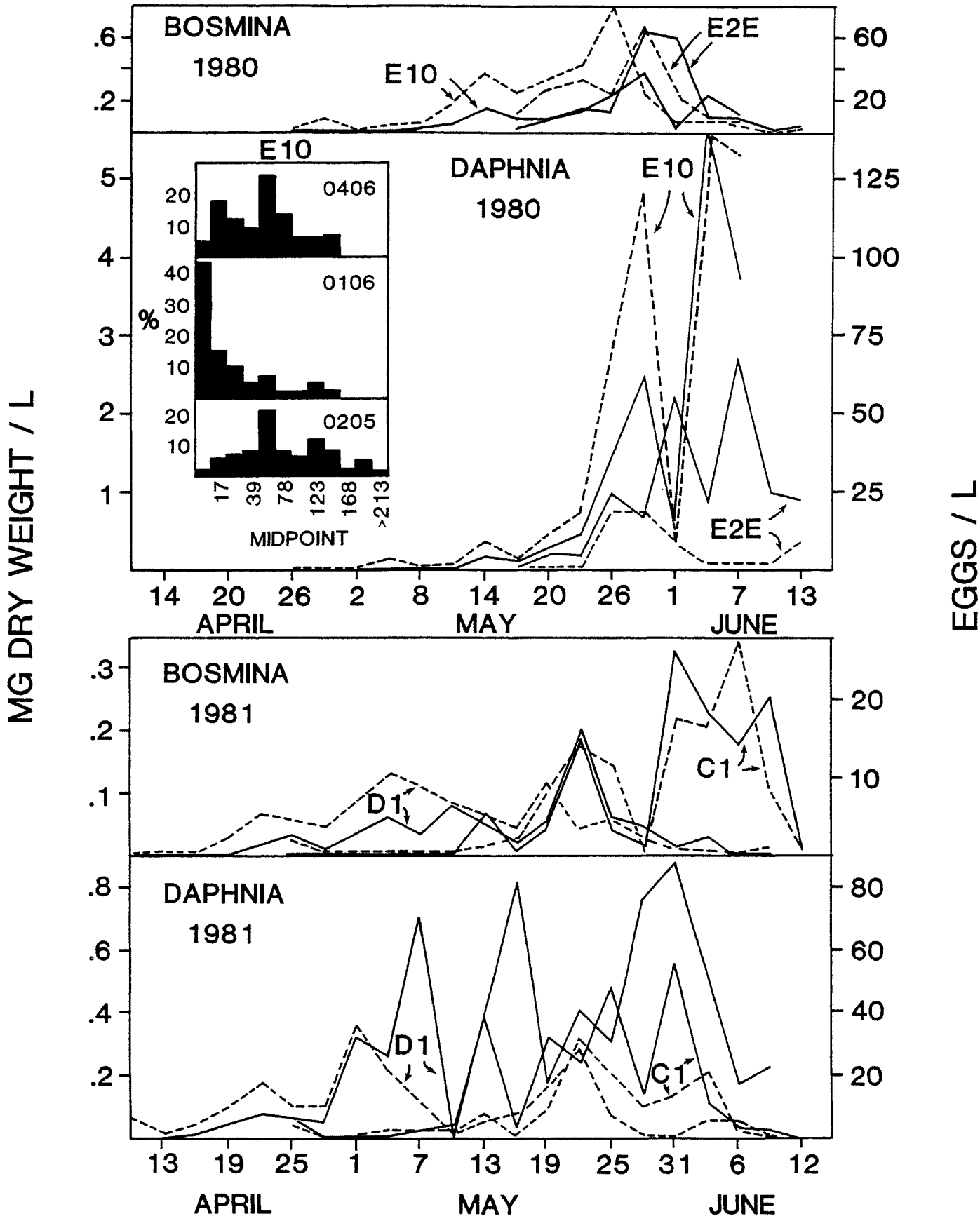

Figure 9. Biomass (———) and egg abundances (- - - - -) of Daphnia and Bosmina in ponds E10, E2, C1, and D1 over time for 1980 and 1981 Inset: Length frequency distribution of alga filaments on May 2, June 1, and June 4, 1980. Midpoint refers to algal length class midpoint in microns.

Discussion

The rates of egg production of Daphnia and Bosmina are dependent upon both the availability of adequate resources and the amount of interfering filamentous algae. For example, Figure 8 illustrates the general declines in pond DI of FR for Daphnia and Bosmina over time. This decline was observed in all ponds regardless of the filament concentration. This decline in FR is due to resource limitation. To separate out the effects of filaments on FR, it is necessary to consider reproductive output when resources are not limiting. Plotting the number of eggs per female of each species as a function of algae per capita available provides an estimate of when resource limitation begins to affect egg production. Pooled data for all ponds for each species indicates that reproductive rates for both species saturate at forage ratios of about 40 ml/mg (Figs. 10, 11). Lampert and Schober (1980) found that egg production in Daphnia pulex saturates at about 0.3 mg carbon per litre. Comparison of this value to the above forage ratio is not possible. However, the egg production of Daphnia in DI shows the same curvilinear response to phytoplankton biomass as did D. pulex (Fig. 10). Bosmina egg production appears to saturate at about the same level (Fig. 11).

Plots of FR versus percentage of filamentous algal volume for forage ratios above 40 ml/mg illustrate the effects of filament concentration on egg production of Daphnia and Bosmina populations (Figs. 12, 13). The value of FR for Daphnia shows a marked decline when filament volumes exceed 20% of total algal volume (Fig. 12), whereas FR for Bosmina is less sensitive to filament concentrations and exhibits fairly high reproductive output at high filament concentrations (Fig. 13). However, the scatter of points in Figure 12 suggests that Bosmina is not immune to very high filament concentrations.

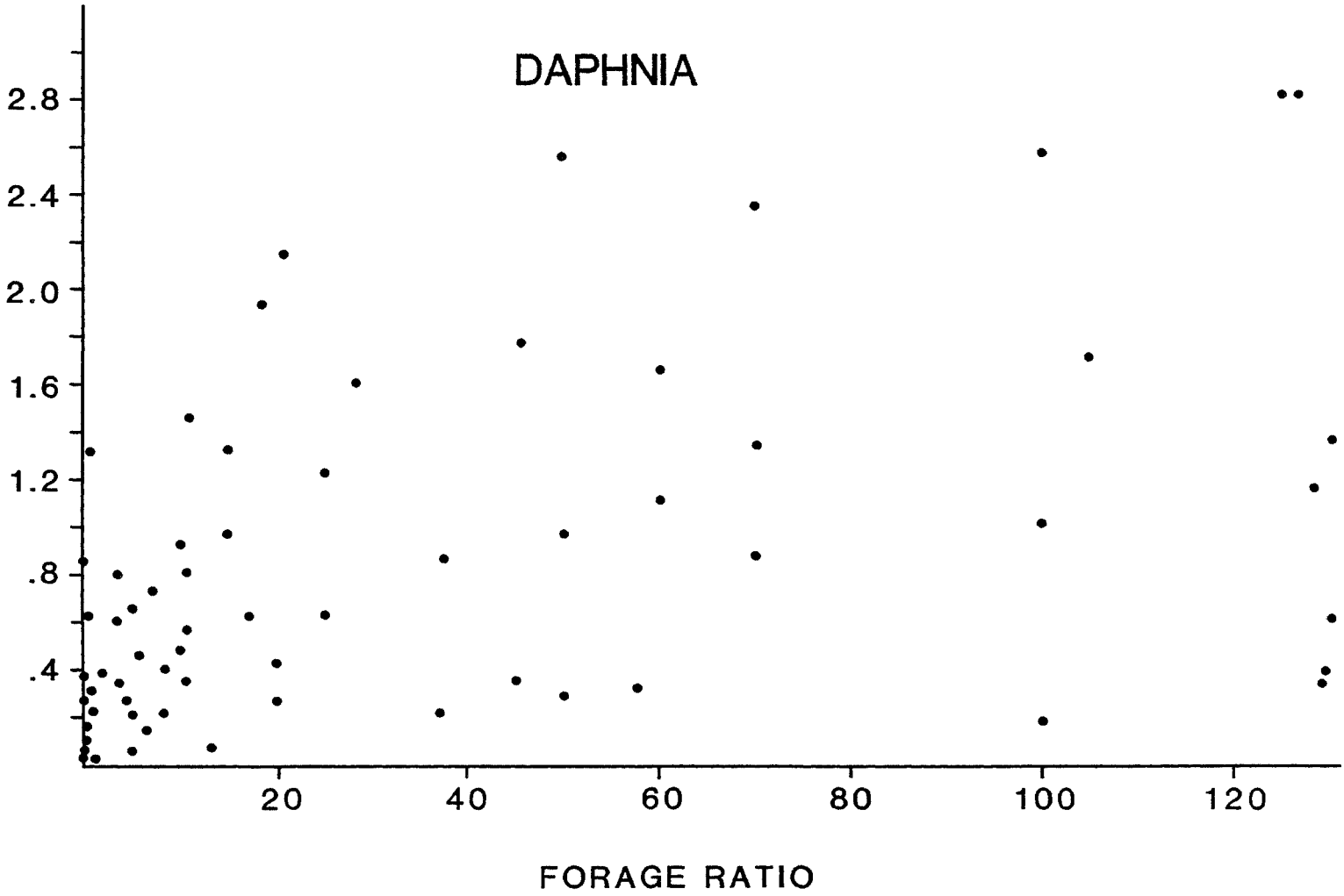

Figure 10. Number of eggs per female Daphnia as a function of its forage ratio. See text for explanation.

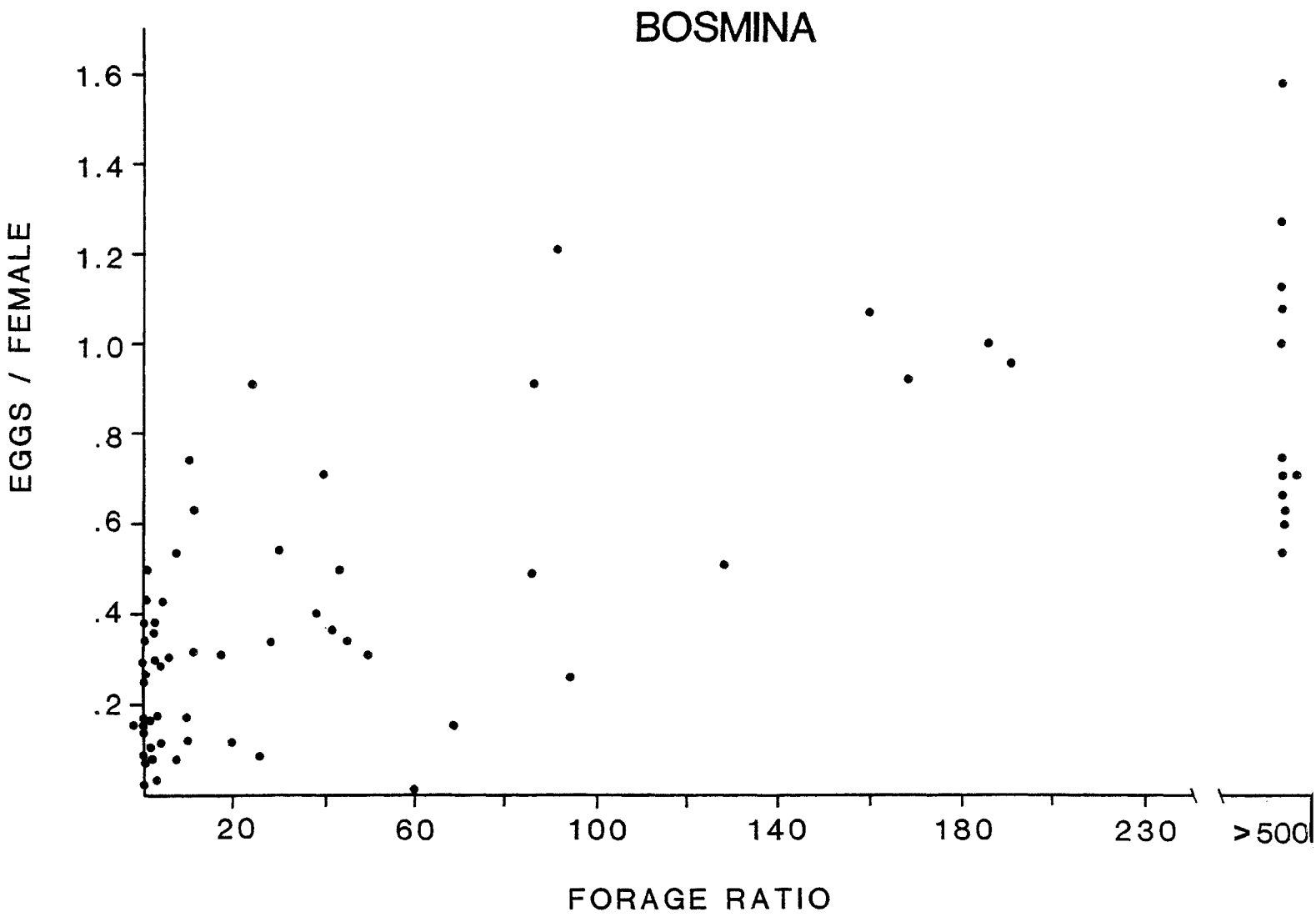

Figure 11. Number of eggs per female Bosmina as a function of its forage ratio. See text for explanation.

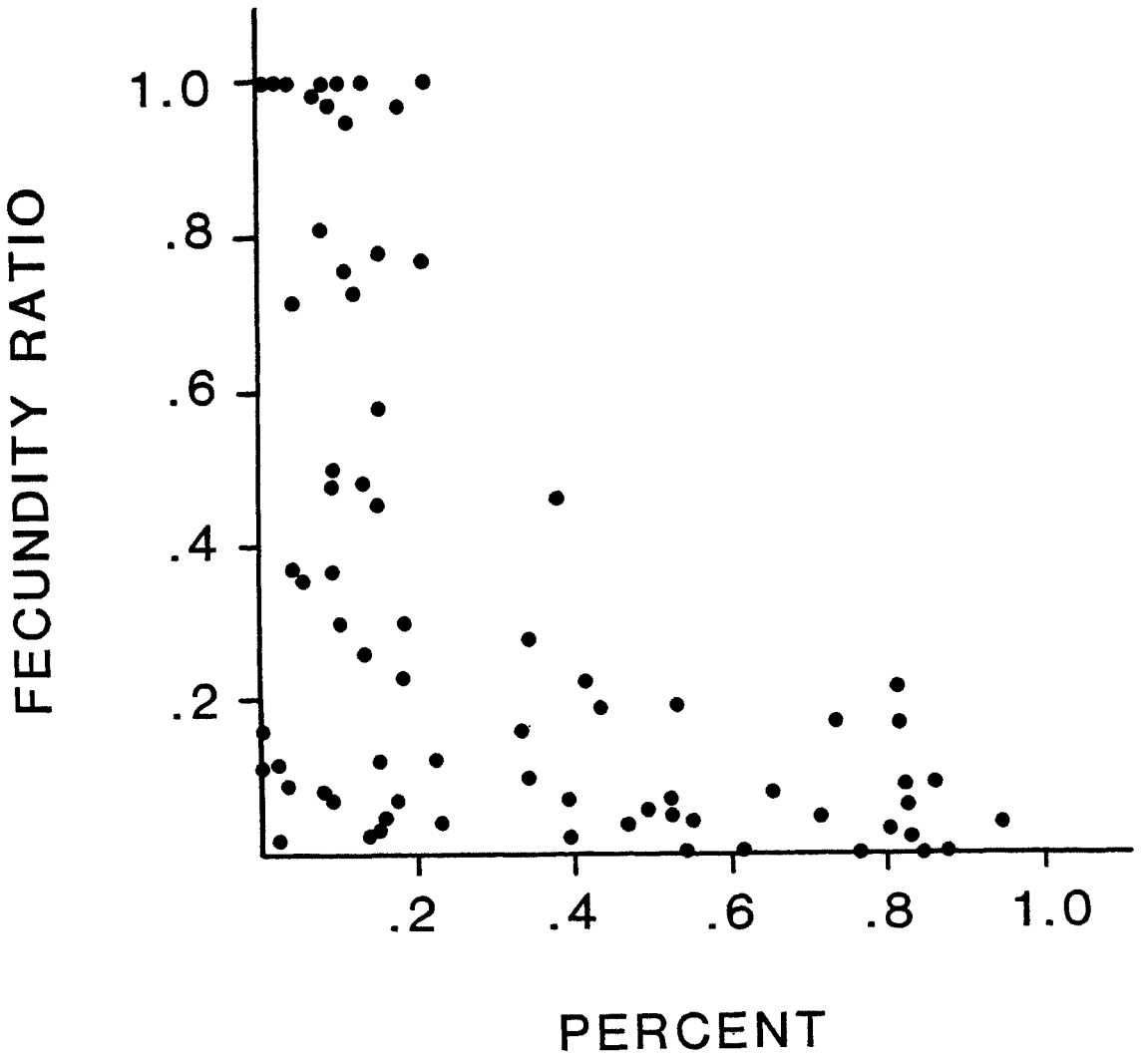

Figure 12. Fecundity ratio (FR) of Daphnia plotted against the percentage of total algal volume as filaments. Above 20% the FR of Daphnia shows a marked decline.

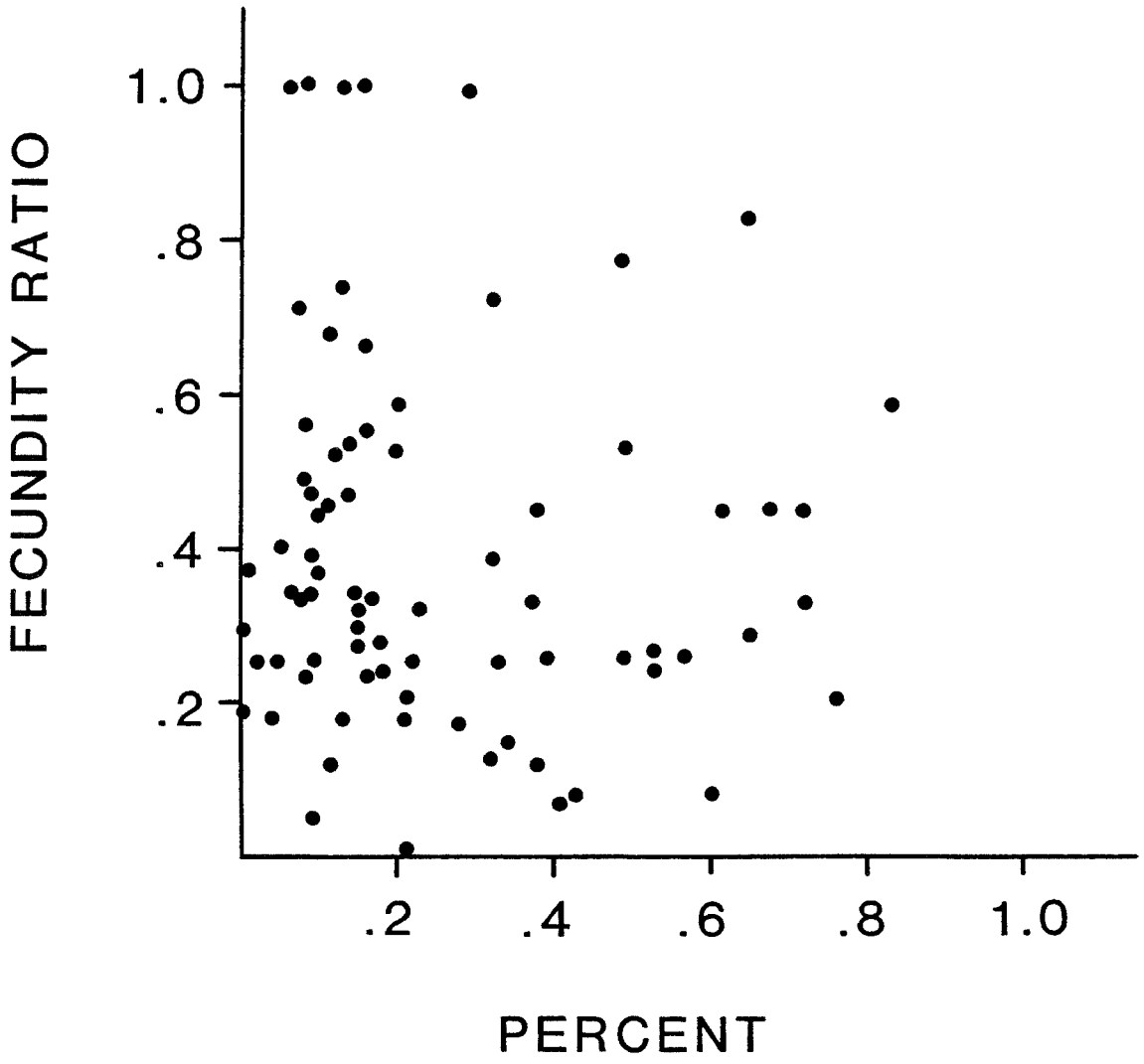

Figure 13. Fecundity ratio (FR) of Bosmina plotted against the percentage of total algal volume as filaments. Bosmina does not show the marked decrease in FR with increasing percentage of filaments as does Daphnia (compare Fig. 12).

Thus the presence of a large abundance of algal filaments inhibited the egg production of Daphnia more than that of Bosmina when PBV volumes were greater than 2 ml/m^3. In the ponds with initially high filament volumes (E10, E2E) the reproduction of Daphnia was always relatively less than that of Bosmina and the increase in filament volumes pond in C1 corresponded with a decrease in the DFR. Conversely, in ponds with low filament concentration (D1, C1) the relative egg production of Daphnia was equal to or greater than that of Bosmina. These results are in agreement with the observations of the effects of filament concentration on the reproductive output of Daphnia in other systems (Gliwicz 1977). In addition, they lend support to Gliwicz's conjecture that Bosmina should be less susceptible to interference by filaments than Daphnia.

The data presented here support Gliwicz's proposed mechanism for the effects of filaments on cladoceran filtering rates. However, large filament concentrations do not necessarily imply competitive advantage for a small filter feeder to the point of exclusion of large filter feeders. Two other factors, namely filament length and ingestibility, must also be taken into account in any proposal concerning the impact of filaments on species succession in the zooplankton.

No systematic study of the ingestibility of algal filaments as a function of length has been performed. Gliwicz (1977) did not report the length of filaments in his lake. Similarly, Porter and Orcutt (1980) did not indicate Anabaena filament lengths in their studies on toxicity of this species to Daphnia. Holm et al. (1983) found that D. pulex ingested single Aphanizomenon filaments up to about 1 mm in length. The length of filaments must have an effect on their ingestibility. The large changes in filament lengths observed over time in pond E10 (Fig. 9) suggests not only that filament concentration but filament length may be of importance to both their effects on filtering rate and ingestibility. Most of the filament biomass in pond E10 on June 1 is in filaments less than 7 um in length. These filaments would not be expected to significantly interfere with the filtering mechanism, are in all probability ingestible, and as such may actually contribute to a daphnid's resource base.

In conjunction with the question of filament ingestibility is that of digestibility. The ability of daphnids to digest blue-green algal filaments has received attention from numerous investigators but the evidence is conflicting. Results from laboratory studies seem to depend on the species of alga used and range from no effects (Sorokin 1968), to survival and reproduction (Arnold 1971), to toxicity (Porter and Orcutt 1980). Clearly it is not yet possible to make a definitive statement concerning the digestibility, and once digested, the effects of blue-green filaments on daphnids.

In light of the above, Gliwicz's (1977) suggested relationship between the increased filament biomass associated with eutrophication and decreases in the size of filter feeders must be considered tentative. Although the short-term effects of filament biomass are suggestive of a selective force, the long term process of species succession is dependent upon a number of different factors. For example, the maximal biomass obtained by both Bosmina and Daphnia in the high filament ponds eventually exceeded that observed in the low filament ponds (Fig. 9). This suggests that long term species succession in the zooplankton cannot be a simple function of algal filament concentration.

CHAPTER V

Effect of Fish Predation on Egg Production in *Daphnia*

Numerous studies have shown that fish selectively remove larger zooplankton and this results in replacement by smaller species (Brooks & Dodson 1965). One possible means by which this could occur is via the removal of the largest individual of a species, those which have the greatest reproductive output per individual. For example, 2 mm *Daphnia galeata mendotae* can carry as many as 36 eggs per clutch, whereas smaller (1.2 mm) individuals of the same species produce a maximum of 3-4 eggs per clutch (Culver 1980). If cladoceran reproduction is controlled by competition for certain food resources, however, moderate predation could actually increase reproductive output (Lynch 1979, Culver et al. 1984). In this study, we examined the seasonal pattern of reproductive output of Cladocera under various intensities of fish predation pressure.

Results

The zooplankton community consisted of Cladocera (*Daphnia galeata mendotae*, *D. parvula*, and *D. ambigua*, and *Bosmina longirostris*), plus copepods and rotifers that were less abundant in terms of biomass particularly after the beginning of May. *Daphnia* abundance (all species combined) was quite variable (Fig. 14a) but was uniformly lower in the two ponds with the highest fish densities. In pond E1 and E2 *Daphnia ambigua* (Maximum Length = 1.1 mm) was dominant, while *Daphnia galeata mendotae* (M.L. = 2.7 mm) and *D. parvula* (M.L. = 1.6 mm) were equally dominant in ponds E4 and C1, and in pond D1 *D. parvula* was succeeded by *D. galeata mendotae* over the season. *Bosmina* (M.L. = 0.75 mm) was present in all ponds (Fig. 14b) and showed a positive relationship to fish density, with extremely high populations in the ponds with the highest fish biomasses.

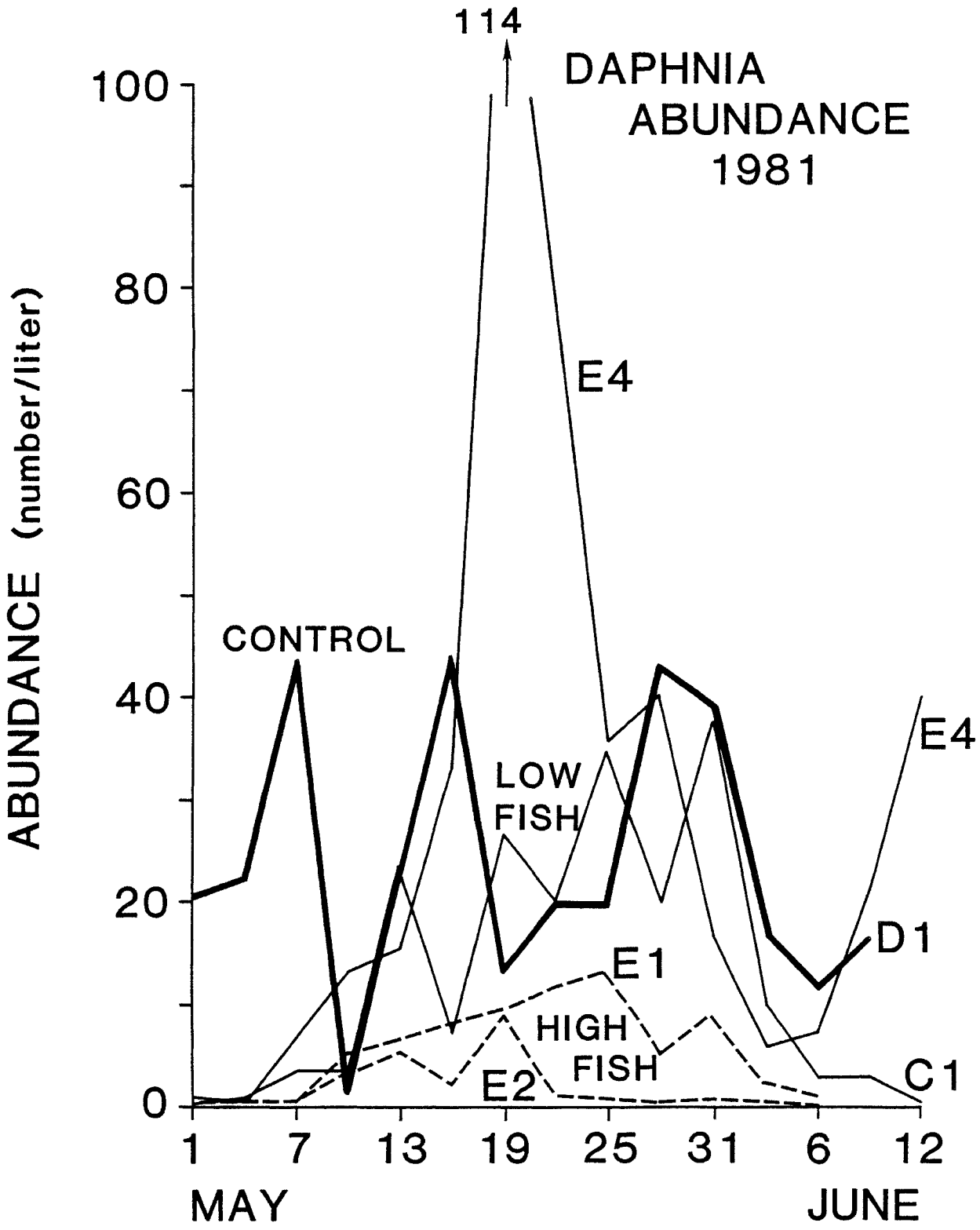

Figure 14 a. Abundance of Daphnia spp in ponds E1, E2, C1, E4, and D1 over time. Daphnia abundance in the high fish ponds was lower than in either the low fish ponds or control ponds.

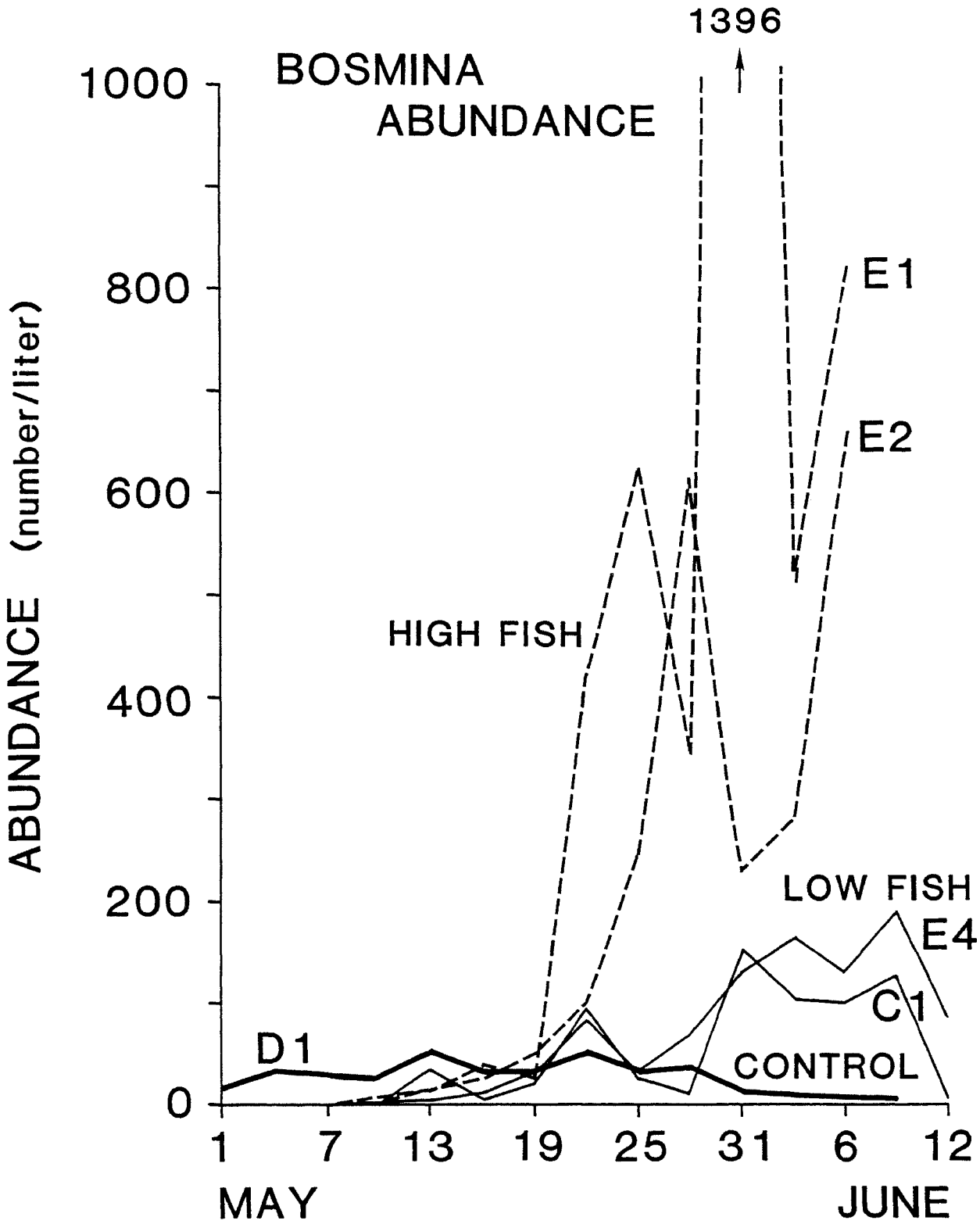

Figure 14 b. Abundance of Bosmina in ponds E1, E2, C1, E4, D1 over time. The abundance of Bosmina was positively related to fish abundance.

The various fish densities resulted in different size distributions for the cladocerans (Fig. 15), with the smallest size distributions occurring in the high fish ponds (E1, E2) and the largest organisms in the control pond. The low fish ponds were similar to the control until the end of May when fish predation removed the largest cladocerans.

Egg production by the Daphnia populations varied over the season, but generally decreased from late April to a mid-May minimum, followed by an increase in late May. When expressed as a percentage of maximal reproductive output, the total egg production was lowest in the control pond, highest in the high fish ponds, and intermediate in the low fish ponds (Fig. 16). This separation is clearest after May 19 with the exception of the population in pond E2, which collapsed after May 25. Fish biomass increased exponentially from initial stocking values to the final values listed in Fig. 15.

Discussion

Predatory mortality was sufficient to keep the abundance of the Daphnia in the high fish ponds below that of the low fish and control ponds (Fig. 14a). In contrast, Bosmina was much more abundant in the high fish ponds than in the low fish ponds, and less abundant yet in the control pond (Fig. 14b). This was a result of relatively low predation pressure on Bosmina and has been reported by other investigators (Zaret 1980, DeMott and Kerfoot 1982). Although this competitive release of Bosmina by fish predation suggests that the Daphnia spp. and Bosmina share a common resource base, other evidence suggests that their resource bases do not entirely overlap in this system (Munch et al. 1984).

The size-frequency distributions of cladocerans seen in these ponds are typical of the pattern seen in all years of the study, with fish selectively removing the larger individuals of the populations. Gut analyses showed that the fish clearly selected larger

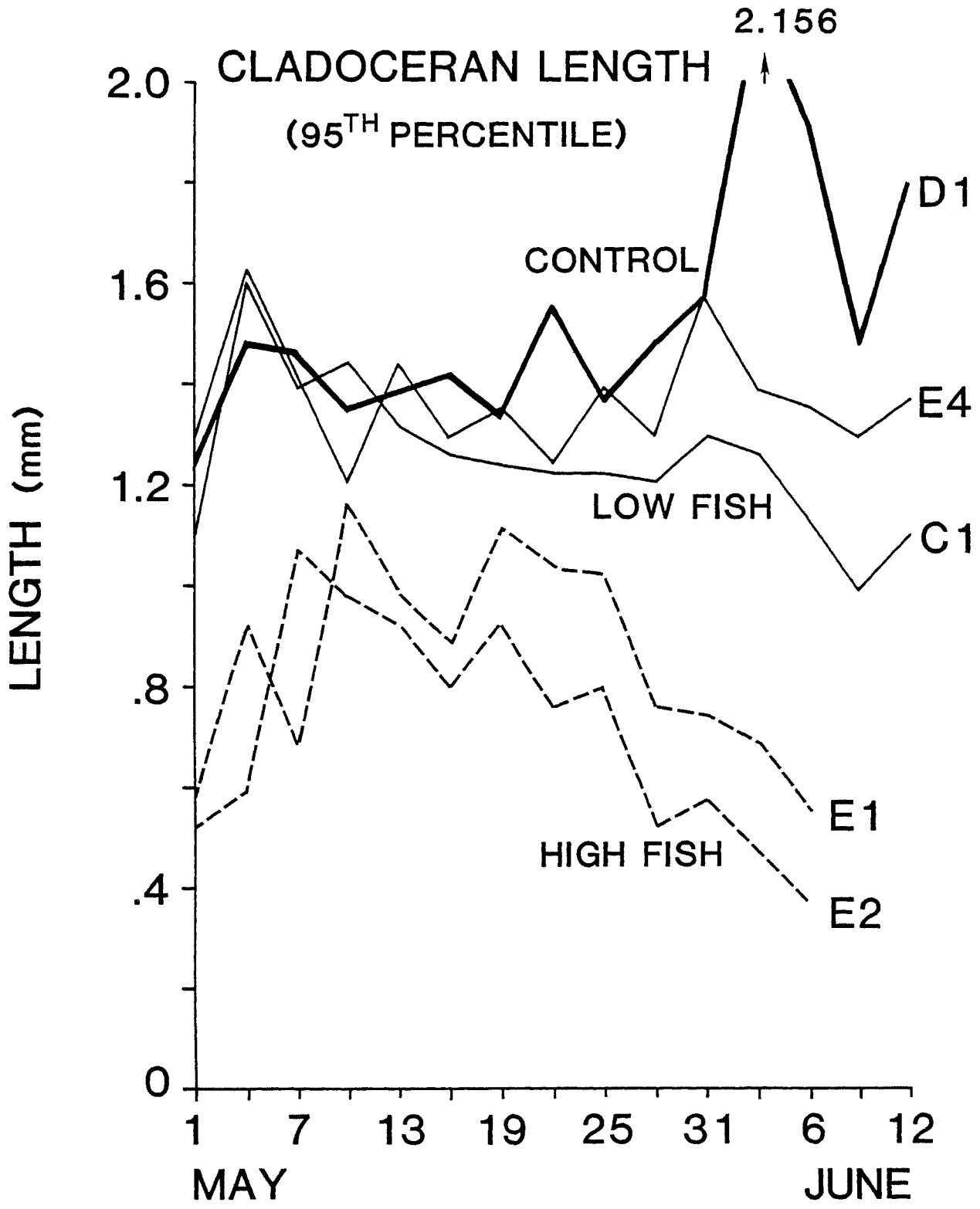

Figure 15. Changes in the 95 the percentile of cladoceran length frequency distributions over time in ponds E1, E2, C1, E4, and D1. The smallest size distributions were found in the high fish ponds. In the low fish ponds the size frequencies were similar to the control until the middle of May, when the fish removed the largest cladocerns.

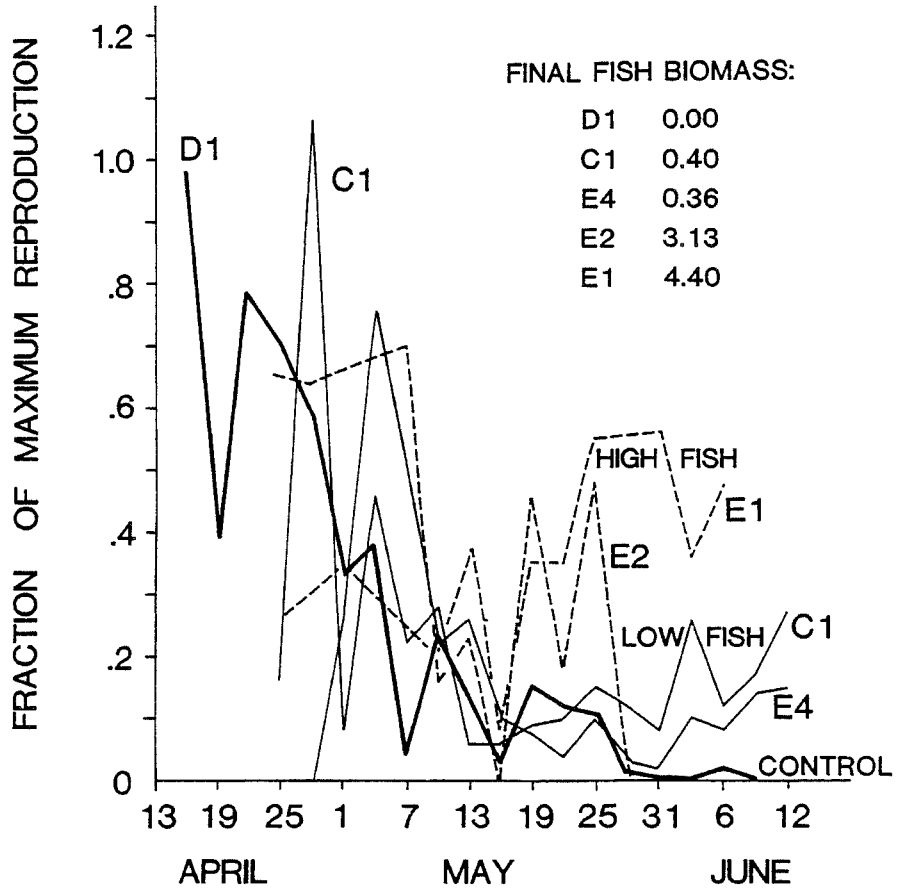

Figure 16. Fraction of calculated maximum fecundity (eggs/female) of Daphnia spp in ponds E1, E2, E4, C1, and D1. Daphnia in the high fish ponds had a higher relative number of eggs/female than in either low fish ponds or the control pond. Final fish biomass is in mg dry weight/m^{-3}.

individuals. Furthermore the large numbers of eggs and ovigerous females in the fish stomachs suggests that ovigerous individuals are selected over non-ovigerous ones (Vaga, unpublished).

The various Daphnia communities respond to increases in predation by increasing reproductive output independent of the composition of the community (Fig. 16). Reproductive output relative to the calculated maximum for the community was greatest in the high fish ponds, lower in the low fish ponds, and lowest in the control pond. Fish remove the larger cladocerans, which in effect increases the resource base available to the smaller forms. This effect is seen until the predation pressure becomes sufficiently great to eliminate most of the adults, where upon the population will collapse, as seen in pond E2.

Whereas the competitive release of Bosmina resulting from predation on Daphnia is predictable based on previous studies (e.g. DeMott and Kerfoot 1982), the increase in reproductive output of Daphnia in the high fish ponds is not. Nevertheless, DeMott and Kerfoot (1982) also obtained an increase in the egg production in their enclosures with fish, and similar results have been reported by Brambilla (1982) and Lynch (1979).

Although the Daphnia abundance data show that high fish predation decreases the abundance of large cladocerans, the egg production data show that when the largest, potentially most fecund individuals are removed from the population, the population responds through an increase in per capita egg production, when there are sufficient resources.

CHAPTER VII

The Effects of Fish Predation and Algal Resource Limitation on Competition between *Daphnia* and *Bosmina*

In recent decades investigations of the forces determining the species composition and dynamics of the zooplankton community have been guided by the paradigms of competition and predation. The predation pressure exerted by fish (Brooks and Dodson 1965) or a combination of vertebrate and invertebrate predation (Zaret 1980) have been proposed as the primary force structuring the zooplankton community. In contrast, Gliwicz (1977) showed that fish predation had a minor impact on the zooplankton in Mikolajskie Lake and suggested that competition among filter feeders was the most important factor in determining the seasonal succession in the zooplankton. Successional patterns were shown to be correlated with changes in the size structure of the phytoplankton community.

It seems more reasonable that in most natural systems both predatory and competitive forces act continuously on the zooplankton community. Thus the question of interest is not which of these forces is the more important but rather what is their relative importance, and further, what determines the magnitude of their relative impact. To investigate this question, field experiments were conducted during 1981 and 1982 to provide information on the effects of changes in the algal resource base (through nutrient additions) and the intensity of fish predation on the structure and dynamics of the zooplankton community. To provide a conceptual framework for data analysis we have constructed a simple model that provides a measure of the relative impacts of resource limitation and predation on the zooplankton. The following sections illustrate the model for the interaction of the two dominant filter feeders in this system, *Bosmina* and *Daphnia*, and discuss the experimental results.

The Model

The number of individuals in each population as function of time is given by,

$$N(t)_i = N(o)_i\, e^{rt} \tag{3}$$

where N_{oi} is the population size of species i at time t, N_o is the initial population size, and r(i) the species-specific instantaneous rate of increase. The value of r is the difference in the instantaneous birth b(i) and death d(i) rates,

$$r_i = b_i - d_i \tag{4}$$

where b(i) and d(i) are time-dependent variables.

The relative growth rates of the two populations can be expressed by their ratio,

$$V = {}^{r(d)}/_{r(b)} \tag{5}$$

where r(b) and r(d) refer to the Bosmina and Daphnia populations, respectively. As a first approximation the value V can be expressed as a function of the sizes of both the phytoplankton and fish communities,

$$V = f(P,F) \tag{6}$$

The scalar surface V gives the ratios of the instantaneous rates of increase of the Daphnia and Bosmina populations as a function of the shared resouroce base and a common predator. Since V is the ratio of two time-dependent functions it is time independent.

At any point on the surface (V) the maximum rate and directions of change of the surface is given by the gradient of (V),

$$V = \frac{V}{P}\ i + \frac{V}{F}\ j \tag{7}$$

where (i) and (j) are unit vectors in the P and F directions, respectively. The above equation defines a vector field that gives that rate of change at any point on the surface (V) in terms of the vector due to the resource base,

$$\frac{V}{P}\ i \tag{8}$$

and due to predator biomass,

$$\frac{V}{P} j \qquad (9)$$

To investigate the relative impact of changes in the resource base and predation pressure it is necessary to define a new quantity (M),

$$M = \frac{V}{P} \Big/ \frac{V}{F} \qquad (10)$$

which is the ratio of the scalar components of the vector defined in equation 7. The value of M at a point on the surface provides a measure of the relative importance of changes in P and F on V. In regions of V where M 1, changes in phytoplankton concentration have more of an impact on V than changes in fish density. The opposite obtains when M 1. When M = 1, V is equally sensitive to changes in phytoplankton and fish densities.

These relationships are illustrated in Figure 17, which depicts the general shape of V that appears to exist in the experimental ponds. The intersection of the plane V = 1 with the surface V defines a curve along which the rates of increase in the two zooplankton populations are equal. At any point on V above this plane Daphnia has a larger r-value than Bosmina and below the plane the reverse is true. Point A is in a region where M 1, indicating that V is more sensitive to changes in phytoplankton than changes in fish density. At point B, V is more sensitive to changes in fish density than phytoplankton density, while at point C, M = 1 and V is influenced equally by changes in both phytoplankton and fish densities.

The above derivation of V is time invariant and therefore does not address the dynamics of the system. This can be accomplished by paramaterizing P and F as functions of time. A point on the surface V can then be given by the position vector R,

$$R(t) = P(t)\, i + F(t)\, j + V(t)\, K + R_o \qquad (11)$$

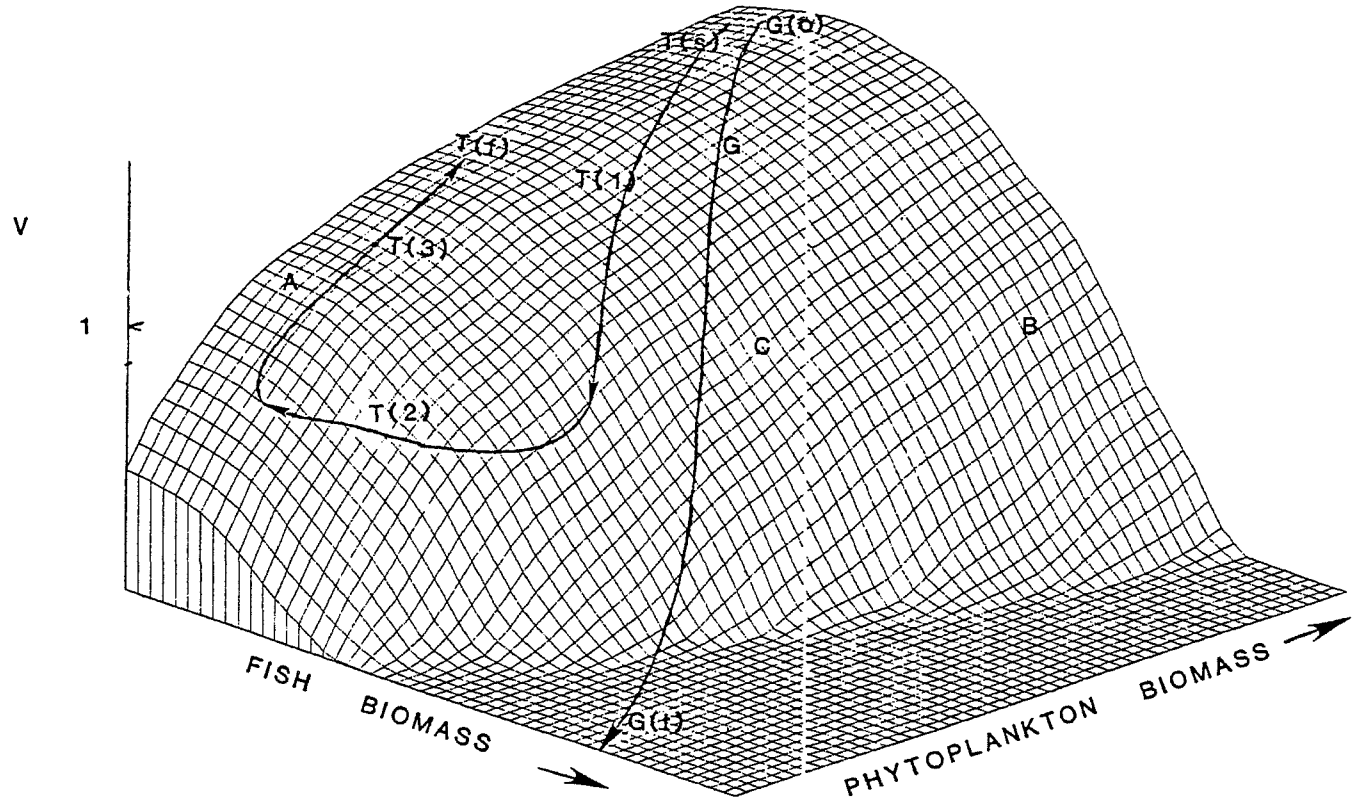

Figure 17. Generalized shape of the response surface V representing the relative reproductive rates of Daphnia.

where R_o defines a set of initial conditions and where F and p are given as functions of time.

$$F, P = f(t) \qquad (12)$$

The value of V at any time (t) is given by the vector R. For any time interval, R traces a curve on the surface V, giving the relative rates of increase of the two zooplankters as a function changes in phytoplankton and fish biomass over time.

Along any curve defined by R(t) the relative effects of P and F on V are given by letting M in equation 10 vary with time.

$$M(t) = f(F,P) \qquad (13)$$

In a system where M(t) is generally less than one, resources will be of greater importance in determining the dynamics of the two zooplankton populations. Predation is of greater importance when M(t) is generally less than one. Explicit measures of the total reproductive output of both zooplankton populations have been derived as a function of the trajectory of R(t) that defines the conditions under which the two species are expected to coexist. These will not be discussed here.

A description of the interaction of V, F, and P over time in experimental pond (E181) is shown by the oriented curve labelled G in Figure 17. The curve traverses the surface from G to G(t), where G represents the conditions in early spring, i.e. early summer. Over the course of the season, the level of fish biomass increases and the phytoplankton concentration declines. As a result, the value of V progresses over time from a value greater than one to a value less than one.

Discussion

All previous studies concerning the coexistence of Daphnia and Bosmina have concentrated either on the predation or competition aspect of the relationship. The results discussed above represent the first attempt to systematically investigate the effects of both competition and predation, and suggest the general conditions necessary

for coexistence. Consider the hypothetical curve T on surface V (Fig. 17) which represents the dynamics observed in most north temperate lakes. The point labelled T(s) is early spring and T(f) is late summer. Line segment T(1) describes the course of events during the spring, when phytoplankton concentrations are high (and decreasing) and larval fish biomass is low (and increasing). Segment T(2) occurs in midsummer, when phytoplankton concentrations are low and fish predation is decreasing as the larval fish switch to a piscivorous feeding mode. Segment T(3) is the situation seen in late summer when phytoplankton concentrations increase with autumnal circulation and fish predation is minimal. The trajectory of T suggests that the coexistence of Bosmina and Daphnia in north temperate systems is relatively insensitive to fish predation.

CHAPTER VIII

Larval Fish Mortality and Management Recommendations

Introduction

Recreational fishing is a significant use of water resources in the state of Ohio, particularly for gamefish species. Many species are raised by state and federal fish hatcheries in order to maintain populations of these species in established waters where conditions are not favorable for reproduction, to introduce them to newly-constructed impoundments, or to re-establish them in areas where they have become scarce for any of several reasons (e.g., over-fishing and pollution, etc.). Sauger stocked in Lake Erie in the past few years, for example, have grown to exceptionally large size, and are eagerly sought by sport fisherman. Sauger and many other gamefish species (walleye, northern pike, striped bass, muskellunge, white bass and some of their hybrids) must be fed live zooplankters during development from yolk-sac to fingerling stage, unlike trout and catfish which can be fed pelletized commercial diets. Accordingly, stocking programs for the former species depend upon culture that produces a reliable forage of zooplankton species that can grow and reproduce rapidly enough to survive the predation by rapidly growing fish.

State and federal hatchery operators in Ohio have been unable to raise sufficient numbers of fingerlings of these species due to several problems in the production process, including high mortality of larval fish immediately upon introduction into the ponds, variability in fish production among (Fig. 18) ponds, and crashes in the zooplankton population toward the end of the production cycle. Our project has concentrated on the processes involved in zooplankton growth and reproduction in the ponds, and thus addressed all of the problems except the first one. It should be emphasized that these problems are common to all hatcheries using this type of pond culture (Personal Communications, A. Stoltz, J. Hawkinson, S. Huffaker, C. Lakes).

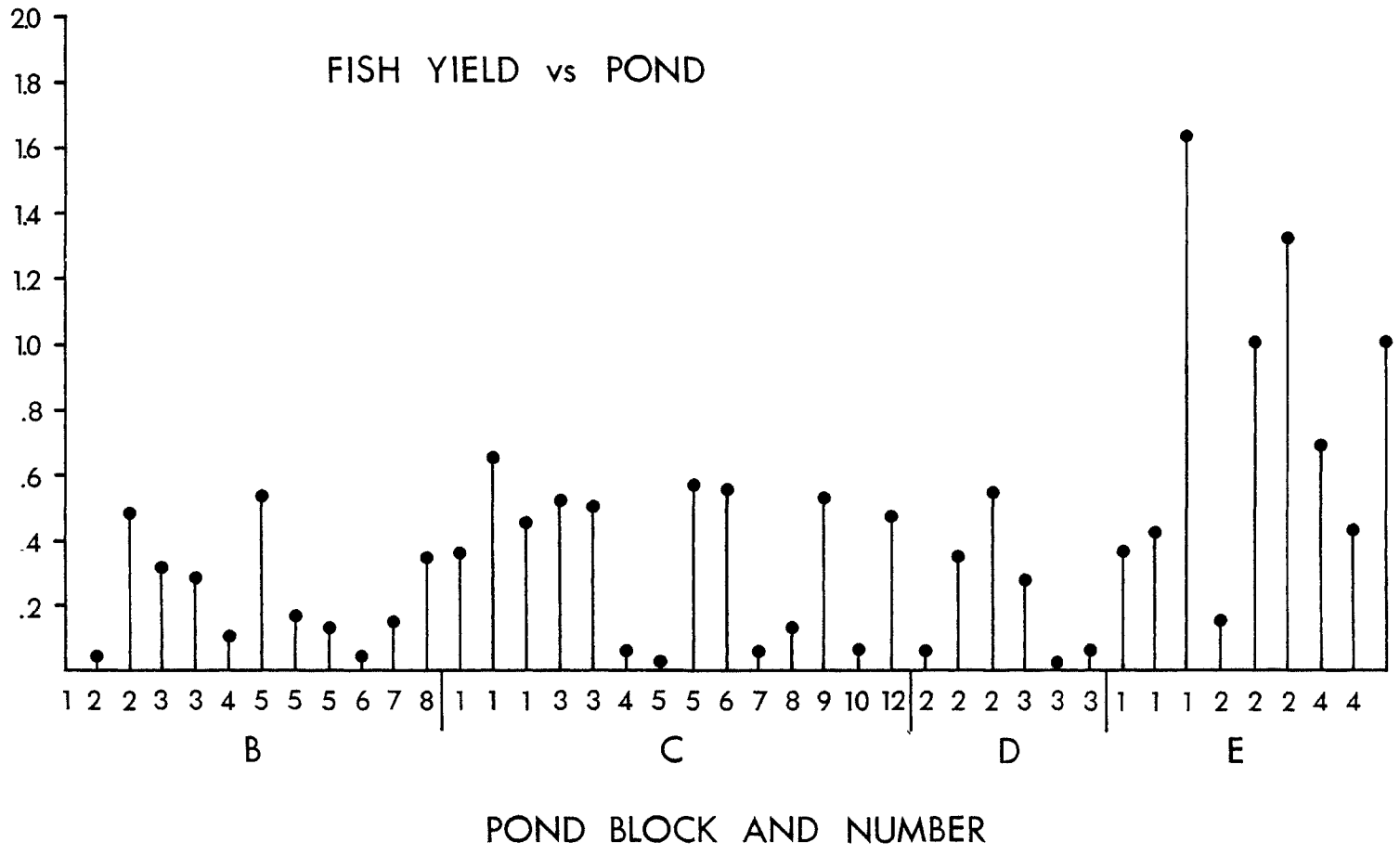

Figure 18. Variability in the yield of fish biomass in different ponds over five years at the Hebron Hatchery. (Data from Hebron Hatchery).

Not only the quantity but also the quality of fingerlings produced is at issue. Fish are often distributed at 1-inch sizes, whereas the states would prefer to have 2 or 3-inch fish which would be less susceptible to predation when newly stocked in a reservoir. Hatchery managers must often harvest the fish stocked at one inch because the zooplankton on which they are raised in the ponds have decreased to a low level. Fish that are held in the ponds after the zooplankton crash lose weight rapidly so that they may be too weak to adapt to their new environment after stocking. If their reserve is used up in the hatchery ponds they may starve before they locate appropriate food sources in the reservoir. The lack of flexibility on harvest times from the ponds also gives the hatchery manager very little choice about when the ponds are drained. Limitations on the total volume of water that can be drained from the hatchery at one time, personnel available to handle the fish, holding facilities, and transport to the lake to be stocked all make it advantageous to be able to extend the time fish can be held in the ponds to $\pm$ one week instead of the 48 hrs currently available.

The cost of maintaining these hatcheries is relatively large, since they require intensive management of large numbers of ponds (typically 20-40 one-acre ponds) and a good water supply for filling the ponds each spring. The capital investment in ponds, drains, etc. is on the order of millions of dollars per hatchery, but the value of the product is also significant. The value of each fingerling depends upon size (Table 4), and is high enough that the 100,000 stocked per pond in each of 40 ponds yield a potential output of over a million dollars worth of fish--if each fry survives to be stocked in one inch in size, and much more if each survives to three inches. Variations in survival and the size at which the fish must be harvested contribute decidedly to the cost-benefit ratio of the hatchery operation, all of which depends upon zooplankton production in the ponds. The economic impact of improving the reliability of zooplankton production in the ponds is thus considerable, particularly when one considers the hundreds of fish hatcheries of this type in North America.

TABLE 4

SUMMARY OF FISH VALUES

Length Species	1"	2"	3"	4"
Pike	$0.30	0.60	0.90	1.20
Striped Bass	0.30	0.50	0.80	1.10
Walleye	0.35	0.45	0.60	1.00
Sauger	0.35	0.45	0.60	1.00

(Source: Reimbursement values for fish. Prepared by the Monetary Values of Fish Committee, North Central Division, American Fisheries Society, 1978)

Results

A summary of data from one pike and one sauger pond for 1980 is presented in Figure 18. Physical parameters of the ponds showed similar trends over the season. With the exception of two cooling periods, the water temperature increased steadily throughout the season (Fig. 19). The minimum temperature (8.2°C) was recorded on 14 May and the maximum (25.5°C) on 7 June. Oxygen concentrations ranged from 6-15 ppm and were never significantly depleted near the sediments. Secchi transparency increased continually in ponds as did total insolation. Total phosphorus concentration increased dramatically in the pike pond during the beginning of May but was at a constant high level throughout May and the first part of June in the sauger pond. Data from the exclosures were similar to those for the open water

Calculated rates of biomass transfer from zooplankton to fish reveal that in the pike pond the fish harvested less than 30% of available zooplankton biomass. During the final week of growth (29 April - 5 May) the growth rates of both fish and zooplankton

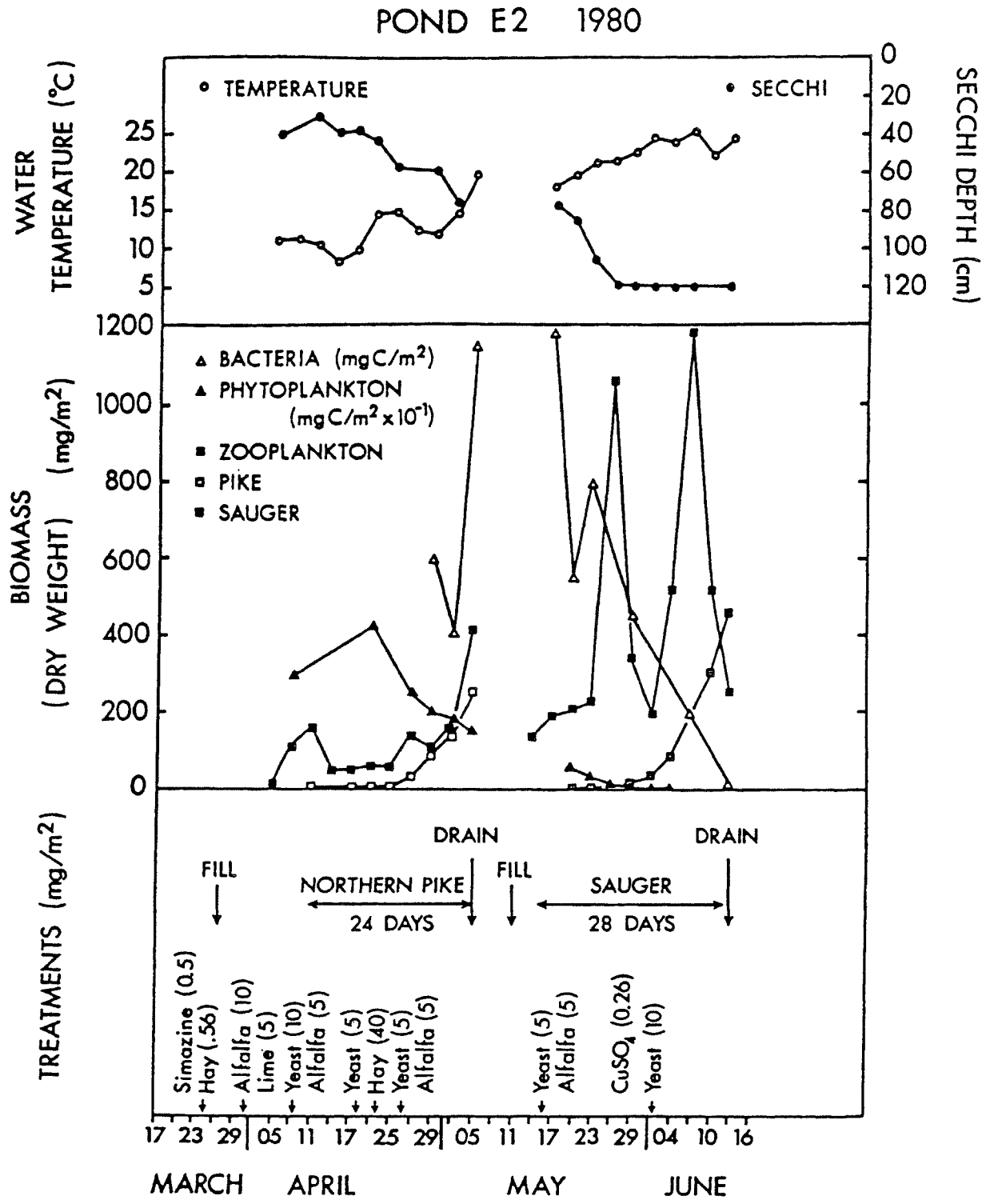

Figure 19. Top Panel: Temperature and Secchi depth for pond E2 1980. Middle Panel: Biomasses of the various trophic components in pond E2 1980 over time. Bottom Panel: General schedule for Pone E2, including fish species, timing and amounts of fertilizer additions.

were similar in magnitude (25 and 38 mg dry wt./m^2-day, respectively) but the fish yield was 118 mg dry wt./m^2 while the zooplankton biomass was 440 mg dry wt./m^2.

Similar calculations for the sauger pond indicate that zooplankton biomass was again underutilized. The subsequent large biomass peak on 7 June was followed by a dramatic decrease (7-13 June). The large decline was only partially due to fish predation. The zooplankton biomass declined on an average of 111 mg dry wt./m^2-da during this period. The consumption of zooplankton biomass by fish averaged about 60 mg dry wt./m^2-da. Thus fish predation accounted for about one-half of the zooplankton biomass decline. The balance of the loss can be accounted for by resource limitation, i.e. the algal and bacterial food base was overgrazed by the zooplankton. This is reflected in the decline in both the numbers of algae and bacteria (Fig. 19).

During the 1981 field season two walleye ponds were used to investigate the effects of inorganic fertilizer on the trophic relationships in the pond. Inorganic fertilizer (7.7 kg, N:P:K 10:1:1) was added to pond E1 at weekly intervals beginning 12 days after the addition of fish. Pond E2 served as the control. The treated pond showed generally higher levels of primary productivity, larger numbers of the dominant zooplankton species (Daphnia spp., Cyclops vernalis), as well as a 22% larger final fish biomass. More importantly, the rate of fish biomass increase in pond E1 was 36% greater than in pond E2. This indicates that the addition of inorganic nutrients stimulates primary productivity and further that this increase in productivity is passed through the zooplankton to the fish.

Trophic analyses of this kind revealed that the fish yield per pond over all years of the study has not correlated with any major environmental variabies, e.g. phytoplankton biomass, primary productivity, zooplankton biomass. For example, the realtionship between fish survival rate and maximal zooplankton biomass showed no trend (Fig. 20).

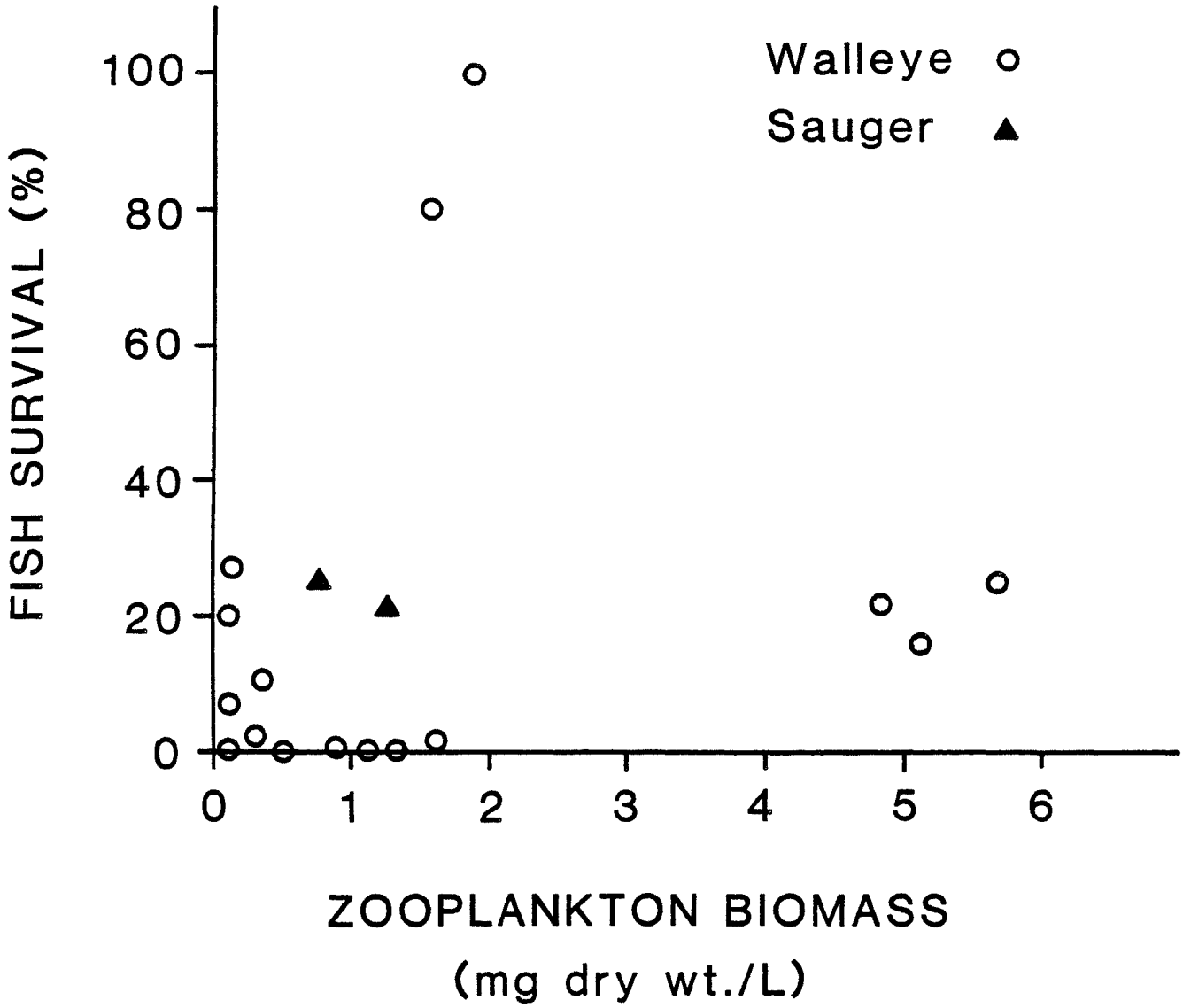

Figure 20. Percentage survival of Walleye and Sauger as a function of maximum standing crop of zooplankton. The number of fish surviving had no relationship to the standing crop of zooplankton.

The species specific survival rate as function of initial stocking density was constant at about 25% for Northern Pike, varied from 20-100% for Walleye, and was uniformly less than 20% for Sauger (Fig.20).

Discussion

Our analysis of both the cool (pike) and warm (sauger, walleye) water systems allows some generalizations to be made concerning the trophic dynamics of fish rearing ponds. The natural system (i.e. no treatments) in these small ponds tends to build up algal biomass during the spring and early summer mainly as a function of increasing temperature and insolation. This build-up is utilized by filter-feeding zooplankton which eventually overgraze the algal/bacterial food base. Thus we observe a characteristic peak in algal biomass followed by a peak in zooplankton biomass. The zooplankton decline begins about the time the fish predation becomes a significant drain on the zooplankton community. This results in a precipitous decline in the zooplankton biomass, with a significant portion of the zooplankton biomass being lost from the system. This inherently unstable pattern of growth and decline is determined by the growth-rate characteristics of algae, bacteria, zooplankton, and fish as well as the transfer rates between successive trophic levels. While variable in detail this pattern appears to occur annually and indeed is similar to that seen in many north temperate lakes.

The absence of correlations between fish yields and environmental variables indicates the presence of some other factor(s) that significantly affect fish mortality in the ponds. The stocking and handling techniques discussed above for the larvae coupled with the inherent survival rate of these species is to a large extent responsible for the observed variability in fish yield and to overall low hatchery output.

The survival rate of the three species of larvae are quite different from one another. Northern Pike larvae have a survival rate of about 25%, Sauger have a consistently low survival rate which seldom exceeds 10%, and Walleye exhibit a wide

range of survival. These differences can be traced to the sensitivity of the eggs and fry to handling. Pike have the largest eggs and therefore have more yolk per fry. In addition, the egg membrane of this species appears to be more resistant to damage than the others and the fry are also able to withstand traumas associated with handling to a much greater degree. This accounts for their survival rate over different years being independent of stocking density (Fig. 21).

In contrast to Pike, both Walleye and Sauger have smaller eggs with less yolk per fry. The Walleye and Sauger differ in that the eggs and fry of Walleye are both able to withstand handling better than Sauger. The Walleye have an inherently higher survival rate but are susceptible to handling mortality. This is reflected in the high variability seen in the survival rate (Fig. 21). On the other hand, Sauger eggs and fry are extremely sensitive to handling and probably also have an inherently low mortality due to the frailty of the fry. The nature of the most important factors contributing to this low survival is unknown, but the eggs of this species can exhibit mortalities of 50% or more in one day. Thus the consistently low survival of this species (Fig. 21) appears to be to its inability to withstand handling.

To summarize, Northern Pike are relatively insensitive to handling trauma and have a survival rate of about 25% which is probably close to their natural mortality. Walleye have a much higher potential survival rate that Pike but at the same time are more sensitive to handling. Therefore this species production is highly dependent on the methods used during the stocking procedure. Sauger are so sensitive to handling their survival has not exceeded 20%.

Management Recommendation

Based upon the results of this three year field study we can make the following recommendations for modifying the existing protocols for the handling, stocking, and raising of Northern Pike, Walleye, and Sauger.

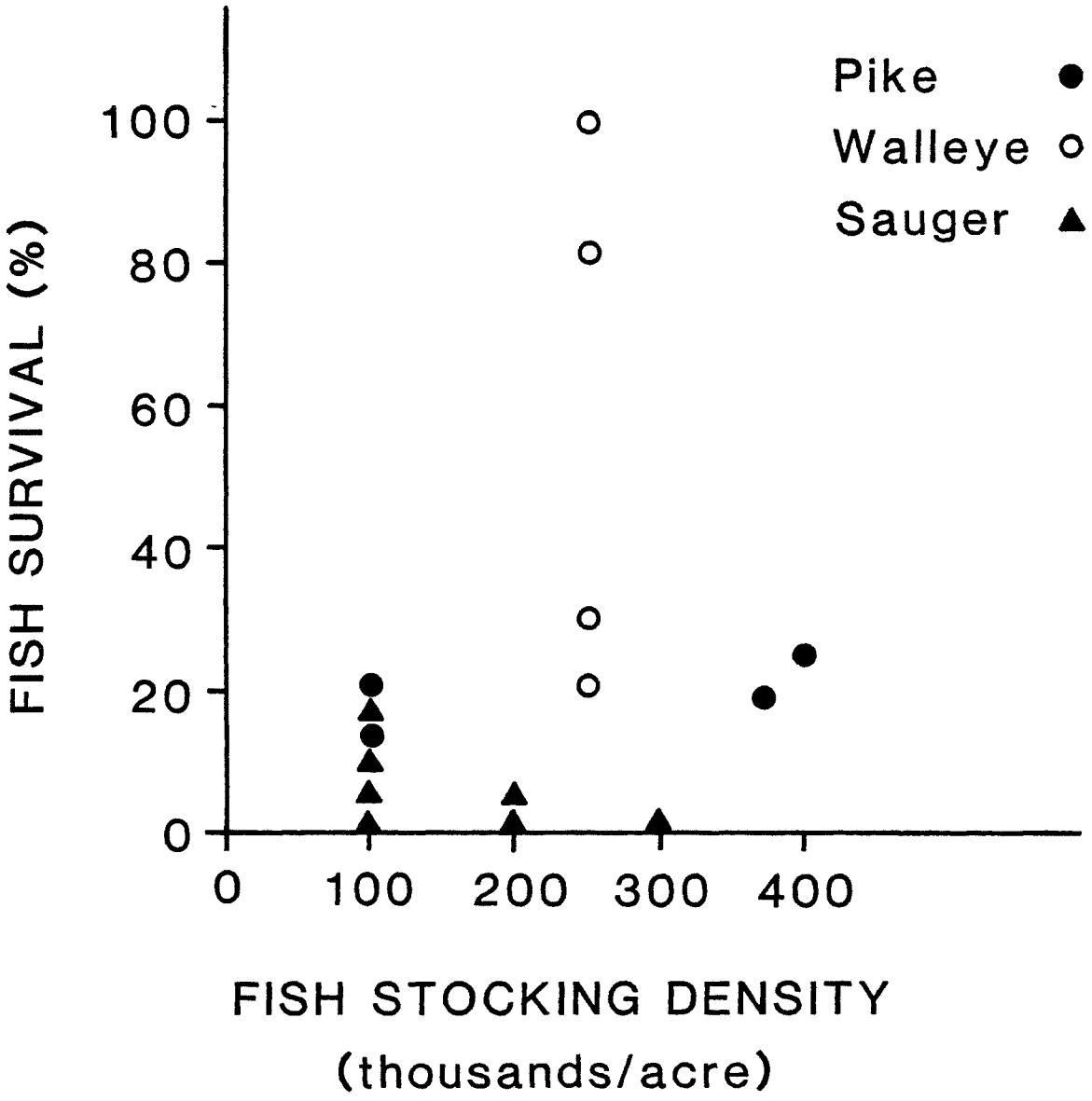

Figure 21. Percentage of fish surviving as a function of the initial stocking density. Only Walleye showed a response to increasing the number of fish stocked per pond. (see text).

1. Increasing the stocking density of all species. From considerations of the trophic structure of the Hebron System, it is apparent that the zooplankton forage base is consistently underutilized. For Pike we suggest an initial density of 300,000 fry per one acre pond, Walleye at 250,000 per acre. The survival rate of Sauger is so low that it is not possible to suggest a reasonable stocking density that would provide reasonable returns (see Prospectus). These modifications alone would increase hatchery output by about a factor of two.
2. Determining the blue-green algal filament concentration in the inoculum water before filling the ponds. The magnitude of the filament load in system materially affects the dynamics of the zooplankton and must be taken into account in the determination of the inorganic fertilization regime.
3. Increasing the use of inorganic fertilizers (phosphorus and nitrogen). Use of inorganic fertilizers increases the level of primary productivity and the size of fish at harvest (for a given stocking rate). Additions of fertilizer, however, should be applied in small serial doses (e.g. 5 pounds of 10:1 phosphorus:nitrogen 3 times per week) and only when the blue-green filaments comprise less than 20% of total phytoplankton biomass. If fertilizer is added when a significant filament biomass is present this will result in a bloom of filaments which is counter productive to secondary production and fish productivity.
4. Stocking fish into ponds at the egg stage rather than at the swim-up stage. Placing the fish into the ponds as eggs obviates the need for handling them at the swim-up stage. The eggs of all species are better able to stand handling than the fry.
5. Eliminating the use of organic fertilizers. Exclusive use of inorganic fertilizers will maximize hatchery output and also reduce operating expenses (Table 5). While efficacy of organic fertilizers is at this time problematic, the use of inorganic fertilizers reduces expenses significantly without reducing fish production.

In summary, the present trophic structure of the Hebron System is able to support approximately the number of fish stocked under the present regimen, assuming 100% survival, e.g. 25 fish/m^2. The data show that due to a combination of factors other than food limitation the survival of these species is generally much less than 100%. Furthermore, the trophic system can support at least twice the fish biomass that is on average currently harvested. Therefore, the hatchery output of these species could be increased by a factor of two simply by increasing the number of fish stocked per pond by the same factor.

Implementation of the management plan being developed here will significantly improve the cost-benefit ratio of fish culture in the state of Ohio and elsewhere. This improvement stems from two sources:

1. Reduction in the absolute cost of hatchery operations. The cost of fertilization per pond is reduced when inorganic fertilizer and active yeast are used in place of the current organic fertilizers (hay, alfalfa meal, brewer's yeast). For example, in two experimental ponds studied, the fertilizer cost per pond was reduced by 44%-72% as compared with normal organic fertilization (Table 5, Column A).

2. Increasing the absolute yield of fish biomass per pond. A comparison of fertilizer cost per unit fish yield is presented in Table 5. With a decrease in cost and an increase in total output the cost per fish dropped from 0.40¢ to 0.06¢ per fish for walleye and from 0.33¢ to 0.019¢ for pike in the ponds fertilized with inorganic nutrients and active yeast (Table 5, Column B). In terms of biomass the contrast is more dramatic. Production cost of walleye decreased from $3.65./lb to $0.35/lb. while the fertilizer cost for pike decreased from $2.32 to $0.50/lb. (Table 5, Column C).

TABLE 5
COST-BENEFIT ANALYSIS PER POND FOR WALLEYE AND SAUGER

SPECIES	NO. POUNDS (WET WT.)	A TOTAL COST OF FERTILIZER ($)	B COST/FISH (¢)	C COST/LB ($)
		CURRENT FERTILIZATION PLAN (hay, alfalfa, brewer's yeast		
Walleye	52,900	21.9	80.00	0.150	3.65
Pike	16,000	22.8	53.00	0.330	2.32
		EXPERIMENTAL PONDS (inorganic + active yeast)		
Walleye	70,500	135	45.00	0.060	0.35
Pike	80,000	30	15.00	0.019	0.50

CHAPTER IX
PROSPECTUS

This study has provided the most detailed data to date on the trophic dynamics of fish rearing ponds. In addition to providing information of general interest to the aquatic ecologist on the interactions of various trophic compartments it has resulted in some significant discoveries concerning the efficacy of an improvements for current management techniques. Of equal importance are the directions for future research which these data indicate. The following is a brief list of areas that we feel will provide useful information to further refine and improve hatchery management techniques.

1. The ontogeny of fish larvae and their sensitivity to various environmental factors including handling. Since initial egg/fry mortality is the single most important factor in determining the varibility in yield, efforts to quantify the relationships between species specific mortality and changes in environmental variables should prove to be a fruitful avenue to follow in future investigations.
2. Investigation of the detritus food chain. Daphnids are known to be detritivores. Comparison of the efficiencies of the detritus as compared to the algal based food chains would permit a refinement in the current fertilization techniques. At present the efficiency of organic fertilizers is unknown.
3. Artificial seeding of the phytoplankton. At present a majority of the algal biomass is not available to grazers. Experiments directed toward the artificial introduction of edible algal species and manipulation of fertilization may provide a much larger resource base for the zooplankton and thereby increase fish production.

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